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# CHIASMATYPE AND CROSSING OVER

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Two short papers by Janssens, published in the *Comptes Rendus* of the *Société de Biologie* for April and May, 1919, outline an interpretation of the maturation-phenomena in Orthoptera in agreement with his earlier chiasmatype-theory ('09) based on the corresponding phenomena observed in urodeles. It is a matter of so much importance that all phases of this question be fully discussed that we venture to report and examine the conclusions announced in these new communications. For this purpose we have found it convenient to divide the discussion into two parts, one dealing with the matter more from the standpoint of strictly cytological observation, the other more from that of the possibilities suggested by genetic analysis. In order to avoid repetition we have numbered the figures consecutively, but each author is responsible for the part under his name.

## I

### A CYTOLOGICAL VIEW OF THE CHIASMATYPE THEORY

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Professor Janssens's results are as yet illustrated only by diagrams, which leave us in doubt concerning some very important details; nevertheless, a cytologist may be permitted to indicate at this time how the conclusions are related to those of other cytologists who have ex-

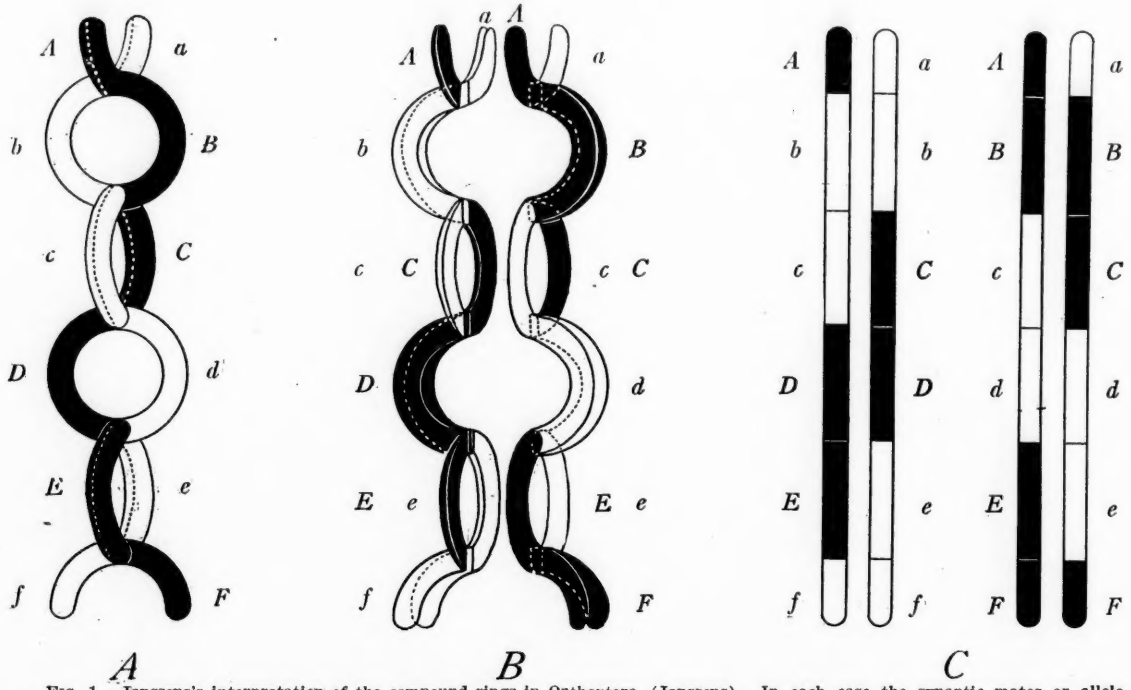


FIG. 1. Janssens's interpretation of the compound rings in Orthoptera (Janssens). In each case the synaptic mates or allelomorphs are in black and white respectively. Corresponding or homologous regions of these mates are designated as *A* and *a*, *B* and *b*, etc. *A*, the ring-series in perspective; *B*, its first division (the second division is at right angles to this, nearly in the plane of the paper); *C*, the four resulting classes of chromatids.

amined the phenomena in Orthoptera and other insects. Incidentally I may remark that Janssens cites from one of my own papers ('12) in support of his general theory and also copies from another ('13) a series of general diagrams by which the theory was illustrated. As he

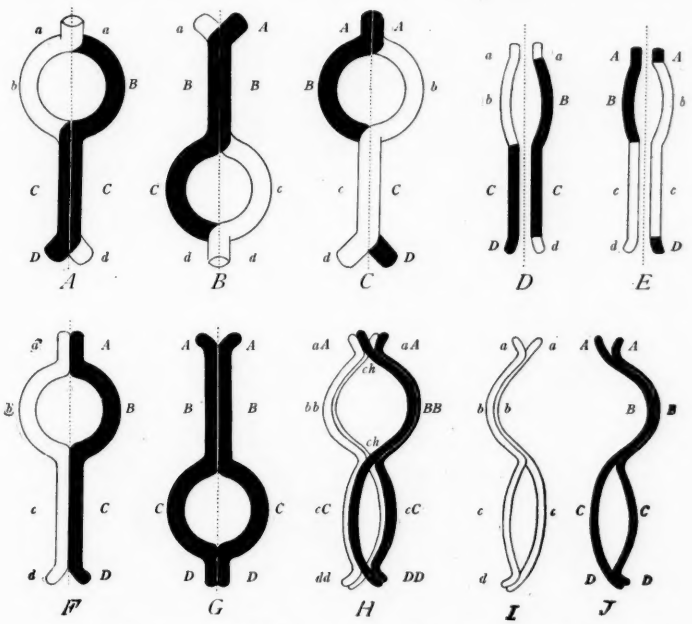


FIG. 2. History of the double rings (*A–E*, after Janssens). In each case the synaptic mates are black and white, respectively, corresponding regions marked *Aa*, *Bb*, etc., as in Fig. 1. *A–E* show Janssens's interpretation of their history. *A*, double ring from one side; *B*, the same rotated 90° to the left; *C*, the same after rotation through 180°; the dotted line shows plane of first division; *D*, *E*, the four resulting classes of chromatids; *F–H*, corresponding figures showing the composition of these rings as heretofore described; *I* and *J*, the two resulting classes of chromatids, with no cross-overs.

points out, these diagrams were too much simplified to give an adequate representation of his views; but a critical account of cytological *minutiæ* was obviously inexpedient in a presentation intended only to make clear to a general audience the nature of Janssens's fundamental assumption. I am glad however to see from these latest

papers that he does not consider the diagrams to have misrepresented the gist of the matter.

So far as can now be judged, Janssens's latest studies add nothing to his paper of 1909 that is new in principle. They are in the main an elaboration of his earlier conclusions concerning the double-ring and double-cross types of tetrads, which were illustrated in his former work by diagrams XI, XVI, XIX and XX. These two forms of tetrads are closely related, and each of them shows in the prophases of meiosis a two-strand chiasma —*i. e.*, two threads which seem to pass over from one synaptic mate to the other, crossing each other midway between them, as in Fig. 5, I or 5, III—such as formed the main basis of the original chiasmatype theory. It may be needless to describe these tetrads, which are perfectly familiar to cytologists, but for the sake of clearness I will briefly review their composition as now generally understood.

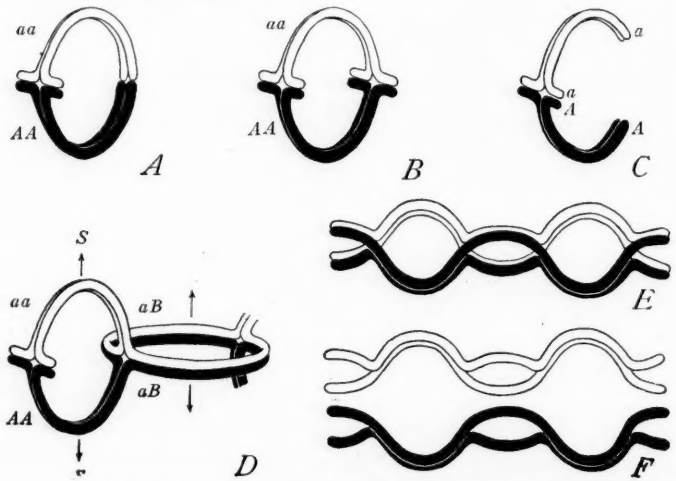


FIG. 3. Diagram to show relation between the single rings, double crosses, double ring and multiple ring types of tetrads. In each case the synaptic mates are black and white respectively. *A*, single ring with one pair of lateral arms; *B*, same with two pairs of arms; *C*, double cross type with curved arms; *D*, double ring, showing spindle-attachments (*S*, *S*); *E*, multiple ring type (viewed in somewhat different perspective); *F*, mode of division of such a tetrad.

Ring-tetrads may be single, or may consist of two or more rings joined together in such a manner as to be successively at right angles to one another, as is schematically shown in Janssens's diagram, here reproduced in Figs. 1 and 2 *A–C*. Single rings of the type here in question (Fig. 3 *A, B*) were I think first clearly described and figured in my laboratory by Paulmier ('98) in Hemiptera, though he did not correctly make out their mode of origin. Similar rings were subsequently studied in many other animals, *e. g.*, in Orthoptera by McClung, Sutton, Granata and others, in urodeles by Janssens, and in annelids by the Schreiners, Foot and Strobell and others. More recently they have been carefully examined by a number of observers, in particular by McClung ('14), Robertson ('16), and Wenrich ('16, '17). The single ring-tetrad (Fig. 3 *A, B*) consists of a more or less open ring, split lengthwise into two closely apposed halves and cut crosswise at opposite points by two sutures which divide the ring into two semicircular half-rings. The latter are now regarded by practically all observers (Janssens included) as the synaptic mates, joined by their ends but elsewhere widely separated so as to lie on opposite sides of the ring-opening, and each longitudinally split. The longitudinal cleft lies therefore in the plane of the future equation-division, the cross-sutures in that of the reduction-division. At one of the cross-sutures, less often at both, the longitudinal halves of both synaptic mates are commonly drawn out at right angles to the ring (in the manner made clear by Fig. 3 *A, B*) thus forming two lateral arms, each longitudinally double, so that this part of the ring, as seen in face view, offers the figure of a double cross. If the ring be supposed to break in two at the opposite suture and the half-rings to straighten out completely it would become a simple double cross-figure with two short arms and two long (Fig. 3 *C* or 5 III). If, on the other hand, the lateral arms of a closed ring be supposed to elongate still more and to bend away from the original ring until they meet,

they would give rise to a second ring continuous with the first but at right angles to it, as shown in perspective by Fig. 3 *D*; and by repetition of this process would be formed a series of three or more interlocking rings, each at right angles to its successor (Fig. 3 *E, F*).[1] How many such successive rings may be formed is not known. Double rings seem to be the most frequent; but in *Chorthippus* (*Stenobothorus*) both Robertson and Wenrich describe and figure triple rings including at least one case in which the lateral arms are long enough to form a fourth ring, though their ends are in fact free. Janssens's diagram (Fig. 1) represents four complete rings with lateral arms at both ends of the series; and it is quite possible, as McClung has suggested, that some of the forms that have been described as twisted or strepsinema stages may really be early conditions of such multiple rings.

Janssens has found that in the heterotypic division the double or multiple ring-tetrads lie on the spindle with their longer axis transverse to that of the spindle, and establish a lateral (atelomitic or non-terminal) attachment; and since successive rings are always at right angles to one another they lie alternately either in the equatorial plane of the spindle or in a plane at right angles to it, *i. e.*, tangential to the spindle. In the ensuing division the series is cut straight through in the equatorial plane (as shown in Fig. 1), rings which lie in this plane being split lengthwise while those lying tangentially are cut crosswise. This curious result is perfectly in agreement with Robertson's observations on *Chorthippus* ('16, Figs. 179–182) and those of Wenrich on *Trimerotropis* ('17, Plate 3, Figs. 17, 18), and we may probably accept it without hesitation, at least for some tetrads of this type.

Thus far all observers are in agreement concerning the external structure and mode of division of the compound

[1] This account does not correctly describe the mode in which these compound rings actually arise, but it is a convenient way of making clear their structure.

rings. As soon as we look further we encounter what seems at first sight to be a hopeless contradiction between the conclusions of Janssens and those of others.

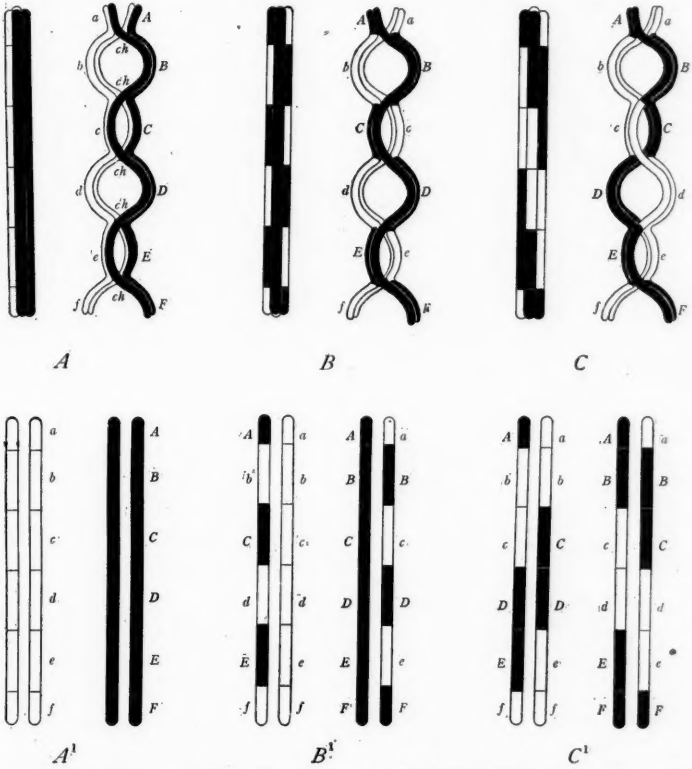


FIG. 4. Diagrams illustrating various possibilities concerning the compound rings, following the outlines of Janssens's figures, but showing also the relations of the chromatids. At the left in each of the upper figures is the longitudinal tetrad-rod from which the ring-series arises, showing results of assumed early cross-overs in $B^1$ or $C^1$. *A*, the compound ring as conceived by McClung, Robertson, etc., with the four resulting chromatids at $A^1$ (no cross-overs). *B*, a compound ring, such as might follow a two-strand cross-over at each node, giving the results shown in $B^1$. *C*, a compound ring giving the results shown in Janssens's diagram (Fig. 1), resulting from a two-strand cross-over between two pairs of threads, in regular alternation at successive nodes. The result ($C^1$) is four classes of chromatids, as shown in $C^1$.

Janssens, holding fast to the general interpretation outlined in his earlier development of the chiasmatype-theory, considers the compound rings to have resulted

from a process of torsion of the synaptic mates about each other, followed by a partial fusion between them at certain points where threads from opposite sides of the spiral have come together, crossing each other to form a "chiasma" at each such point. By a subsequent readjustment of position the regions between these points of partial fusion have opened out to form rings disposed at right angles to one another, and connected at the points where the chiasmas have been formed. The general nature of this rather complicated conception may better be grasped by a study of Fig. 4*C* than from a description. Janssens assumes, further, that *at some period* in their history the rings are cut through at these points of fusion in such a manner as to effect an exchange of corresponding regions between the synaptic mates. The effect, as conceived by Janssens, is shown in Fig. 1 (copied from Janssens), and more in detail in my interpretative Fig. 4 *C, C'*.

Janssens's general interpretation (as will at once appear from his diagrams here reproduced as Figs. 1 and 2 *A–E*) includes two more specific assumptions on which the whole matter turns. These assumptions are: (1) that all the rings are essentially alike, the synaptic mates, or corresponding regions of them (black and white in the figure) lying in every case on opposite sides of the ring-opening, the longitudinal cleft in each thus representing the future equation-division; from this it follows (2), that rings which lie in the equatorial plane of the spindle (horizontally) are divided equationally, while the alternate rings that lie tangential to the spindle are cut crosswise, and hence reductionally, *by the same division*. Both these assumptions differ wholly from the results of previous investigators and hence call for critical examination.

The genesis and later history of the compound (especially the double) rings has been most fully studied in the Orthoptera, having first been considered by McClung and Granata, and more recently investigated with greater

precision especially by Robertson ('16) and by Wenrich ('16, '17). None of these observers, it is true, has traced the history of the rings in every detail; but their results, so far as they go, are entirely in harmony with the better known history of the single rings and double crosses,

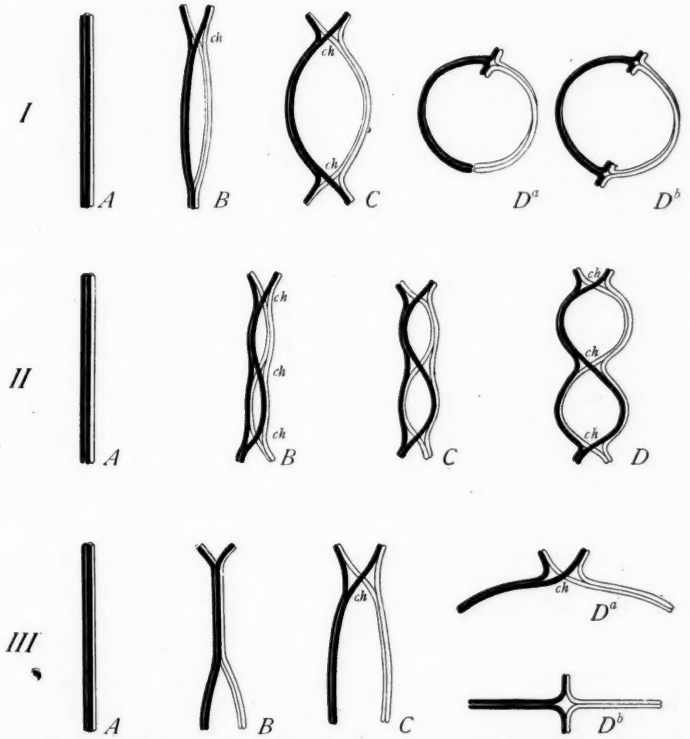


FIG. 5. Diagram (perspective views, from clay models) of the origin of single rings, double rings and double crosses from a longitudinally quadripartite rod. I, single rings; *B* leading to *Da*, and *C* to *Db*. II, double ring-formation. III, double cross-formation; III, *C* derivable from I, *B* by separation of the lower ends of the synaptic mates. In each case *ch* marks an apparent crossing-point or "chiasma."

both of which offer essentially the same problem as the compound rings. These various forms of tetrads arise from a diplotene thread that is at first longitudinally double and sooner or later longitudinally quadripartite

owing to the appearance of a second cleft at right angles to the first. The evidence is nearly or quite conclusive that one of these clefts coincides with the original plane of synapsis or side-by-side apposition of the synaptic mates (also the plane of the future reduction-division) while the other is the equation-plane along which each synaptic mate is longitudinally split.[2] In any case it is generally agreed that single rings arise by the separation and opening out of these threads along *one* of the clefts (generally believed to be the synaptic, as in Fig. 5 I), their ends remaining united, while the second cleft remains as the longitudinal cleft of the ring and represents the plane of the equation-division. The lateral arms of these rings arise, as shown in the figures (5 I, *B, C*) by separation and divergence of the free ends for a certain distance along the second (equational) cleft, thus finally giving the appearance of a double cross at this part of the ring (5 I, *D*).

Double rings, coupled together (Fig. 5 II) arise when the rods separate along different planes in two adjoining regions, the opening of one ring representing the expanded synaptic cleft (appositional or reductional) that of the other the equation-cleft. Such rings are of course at right angles to each other; and as the diagram shows (Fig. 5 II, *B, D*) when these tetrads are viewed obliquely they seem to show at certain points crossed threads or chiasmas (*ch.*) in which two threads cross over from opposite sides.[3] It is of the first importance, however, to bear in mind the fact that *such figures are shown in fore-shortened view.* They are an attempt to represent in two dimensions a figure which actually is in three dimensions. Such tetrads can not adequately be visualized until modeled in clay or by means of wires, so as to be seen in three dimensions. When the models are obliquely viewed they seem indeed to show at each node

[2] This interpretation disregards the possibility (which I think is a probability) that recombination-phenomena or orderly exchanges of material between the synaptic mates may already have occurred in the quadripartite rod; but for the moment we may leave this out of account.

[3] This is clearly shown in McClung's photograph, Fig. 122 ('14).

two threads that are connected by a chiasma and two that are not thus connected; but if the model be rotated through an angle of 90° the appearance is reversed, the "chiasma" now appearing between the two threads that previously seemed unconnected, and *vice versa.*

The same appearance, due to the same cause, is given in early stages of the lateral arm-formation in the single rings (5 I, *B, C*), and is shown with even greater clearness in early stages of the double crosses. The latter arise by separation of the free ends of the four threads from each end towards the middle point, but along different planes (Fig. 5 III, *B–D*), *i. e.,* from one end along the equation-cleft, from the other along the reduction-cleft—a process that is continued until all four threads come to lie in a single plane in the form of a double cross. Here, too, a "chiasma" (*ch*) is very clearly seen; but as in the foregoing cases it is an optical illusion; the models in three dimensions show at once that a straight split through the tetrad involves no transverse break in the chiasma, and that its two strands merely draw apart as the division proceeds. In themselves these figures give no reason whatever to assume that such a break (crossing-over) has taken place at an earlier period or that the synaptic mates have been twisted about each other, as Janssens assumes.

Such an origin of the double or multiple rings seems at first sight wholly inconsistent with Janssens's interpretation; for if it be correctly determined the relation of the synaptic mates to the ring-formation is wholly different in successive rings, as is shown in Figs. 3 *D, E,* 2–*H,* and 4–*A.* Specifically, in case of any two successive rings one always shows the synaptic mates, lying on opposite sides of the ring-opening, and each longitudinally split, while in the adjoining ring half of each synaptic mate surrounds the entire ring-opening, lying in close contact with the corresponding half of its mate. Only in the first case, accordingly, does the longitudinal cleft of the ring correspond to the equation-division. In the sec-

ond case this cleft coincides with the apposition-plane of the synaptic mates (*i. e.,* that of the future reduction-division) while the equation-cleft has opened out to form the ring-opening; and so on in regular alternation. It follows, lastly, that if we disregard for the moment the possibility of an earlier recombination-process, a division that cuts straight through the tetrad, as described alike by Wenrich, Robertson and Janssens, does not in fact divide certain rings equationally and others reductionally in regular alternation but divides the whole series in the same way, either equationally or reductionally as the case may be (Figs. 2 *H, J,* 3 *E, F,* 4 *A*).

In order to make clear the contrast between this conclusion and that of Janssens I have in Fig. 4 *A* followed his outlines but have indicated the course of the four threads (chromatids) in accordance with the account just given. In Fig. 4 *C,* on the other hand, the chromatids are shaded black and white in such a manner as to fit with Janssens's account. A similar comparison is shown for the double-ring tetrads in Figs 2 *F, G,* which follow Janssens's outlines (2 *A, B*) as nearly as possible but are differently shaded; while 2 *H–J* shows the double ring and its mode of division in slightly oblique view, so as to show the "chiasma." In these various figures it is at once evident that although a two-strand chiasma or crossing (*ch*) appears at the junction of every two rings, a straight longitudinal division of such a tetrad (separating black from white) involves on crossing-over, and divides every ring reductionally; *i .e.,* in such a manner as to disjoin the synaptic mates. Here again it is also evident that the multiple ring need involve no twisting of the synaptic mates about one another. It is true that rings of this type, whether single or double, are not infrequently twisted in their earlier stages, and sometimes in their later—a fact long known and easily verifiable; it is shown unmistakably, for instance, in some of my own slides of *Phrynotettix* (from material given me by McClung several years ago). No evidence has yet been pro-

duced, however, to show that such torsion leads to double ring-formation by a process of chiasmatypy. On the contrary, the evidence thus far indicates that the torsion is undone as the prophases advance; and it is a significant fact that in these same twisted rings the free ends of the chromatids (forming the lateral arms) show the typical relation as described above, giving the appearance of a chiasma at each end (as in Fig. 3 *E, F,* or 5 II).[4] Such "chiasmas" (like those seen at the junction of two rings) are not for a moment to be confused with the appearance of crossed threads given in side views of actually twisted rings.

Such is the contradiction—at first sight it seems irreconcilable—between Janssens's conclusions and those of other investigators of these tetrads. These latter results, in particular those of Robertson and of Wenrich, are supported by very detailed and precise studies; and my own observations, particularly on the double crosses, are altogether in favor of their conclusions. Until Janssens's evidence is before us in greater detail it remains to be seen whether the contradiction really is as great as it now appears. In the meantime we may briefly consider certain possibilities which may help to define the issue more clearly.

The conflict of results has not, I think, grown out of the fact that Janssens has worked with a different type of compound ring, though this is possible, nor can we assume that he has not reckoned with the results of other observers. I incline to think that the contradiction may be in the main one of theoretical interpretation rather than of known fact; for in theory all the observed facts may quite logically be interpreted as the result of a chiasmatype that has been completed at a stage prior to the ring-formation. Specifically we might assume that a cross-over has earlier been completed at each node in the series, causing an exchange of two longitudinal halves in

[4] See for instance Granata ('10, Fig. 29), Robertson ('16, Figs. 150*b*, 175), Wenrich ('17, Pl. I, Figs. 8, 9), and Mohr ('16, Fig. 131). The same is clearly seen in my slides.

alternate rings—a process which would produce a condition identical so far as appearances go, in both structure and mode of origin, with the compound ring as described by Granata, McClung, Robertson or Wenrich, but one which has a quite different morphological significance. Such an assumption seems to me to be logically implied by Janssens's own account, though I am not sure that such is actually his meaning.

I have tried to illustrate this by the series of diagrams shown in Fig. 4. *A* represents the compound ring in accordance with the results of McClung and his followers, the synaptic mates being in black and white, respectively. If, however, we assume this condition to have been preceded by a two-strand cross-over or chiasmatypy at each node, the composition of the tetrad becomes that shown in *B* or *C*. Either of these figures realizes the two specific assumptions of Janssens earlier emphasized, namely: (1) that the longitudinal cleft in every ring represents an equation-division (*i. e.*, separates corresponding halves of one synaptic mate in this particular part of the tetrad), and (2) that a straight split through the ring-series (such as is shown in Fig. 1 *B*) will now divide half the rings equationally and the alternate rings reductionally. Both show recombinations in the same regions (*Aa, Cc, Ee*) and in the same relative numbers in the cross-over threads; but they are differently grouped, owing to the fact that in one case (*B*) a cross-over has taken place between the same pair of threads at every node, while in *C* this occurs only at every other node, the cross-overs taking place in regular alternation between two different pairs of threads. As a comparison of Figs. 2 and 4 *C* will show, it is this latter form that corresponds with Janssens's interpretation.

Janssens does not make it clear in his preliminary papers whether he assumes the chiasmas to be cut through during the actual division of the tetrad, though I think is what one would naturally infer from his general account and from his figures, especially of the double

rings (here reproduced as Figs. 2 *A–E*) and of the double crosses (here Figs. 6 *H–C*). On the other hand a study of my Fig. 4 will show that the results of the division, as stated by Janssens himself (my Fig. 4 $C^1$) can only be brought about by a split which passes straight through the equational cleft of the horizontal rings and leaves the chiasma untouched. I infer, therefore, that Janssens does in fact consider the chiasmatypy to have taken place

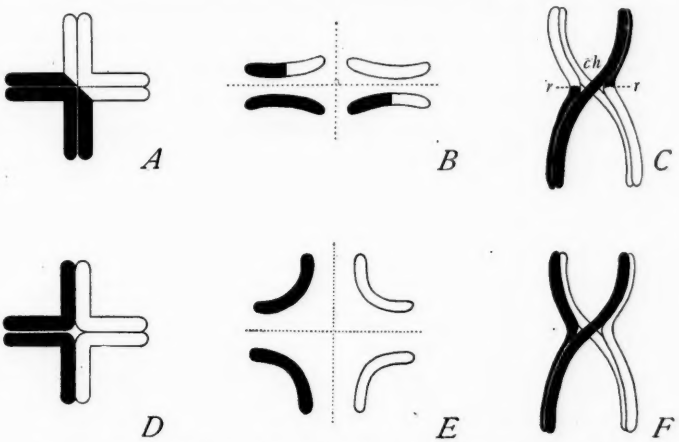


FIG. 6. Interpretations of the double crosses. *A, B,* Janssens's interpretation (from his figures), showing four classes of chromatids, two with a single cross-over each. The result is here the same as shown in Fig. *C* (after an earlier figure of Janssens). *D, E,* the prevailing interpretation of the double cross, with no cross-overs; *F,* early stage of the double cross. (*Cf.* Fig. 5 III, *C.*)

at a stage prior to the opening out and division of the rings; and this would be in agreement with his earlier conclusions, as applied to the tetrads of urodeles, here illustrated by Fig. 6 *C* (after Janssens).[5] At any rate, so far as I can see, it is only by such an interpretation that Janssen's results can be reconciled with those of other observers. More specifically, the assumption must be, I

[5] See Janssens, '09, p. 14 (Diagram, XXII). "We believe that in this case the threads which cross each other are those furthest apart, that is to say, which occupy those parts of the chromosomes that undergo no intermixture. The threads which remain unconnected by a chiasma, on the contrary, are those which have undergone a secondary union at the points where the chromosomes have interpenetrated each other and fused."

think, that the chiasmatypy has taken place during a strepsinema stage prior to the straight, longitudinally divided threads from which the rings arise (Figs. 4 *B, C,* at the left). If now, for the sake of argument, we accept these assumptions, how does it come to pass that the subsequent opening out of the rings exactly fits with the recombination-phenomena that have previously occurred in the tetrad? Morgan has already supplied an answer to this in the ingenious suggestion that *the mode of separation of the threads may be determined by their nature —i. e.,* that the paternal and maternal threads (or portions of threads) may always be the first to separate, however they may lie in the tetrad.[6] This is an important addition which makes the whole series of assumptions logically complete.

All this constitutes a somewhat complicated train of reasoning; nevertheless, if it be granted, it provides formally an escape from the seeming contradiction and leaves the chiasmatype-theory intact. The point, however, that I wish to emphasize is that we have now passed over into a realm of hypothesis and logical construction, based it is true on a vast assemblage of data of the highest importance, but derived from genetic experiment rather than from cytological observation. No observer, so far as I know, has yet seen a process of true crossing-over (recombination) by means of torsion, chiasma-formation, fusion, and secondary splitting apart. That such a process takes place at all remains thus far an inference based on the presence of a continuous two-strand chiasma in later stages of meiosis and on certain resulting appearances in the late prophase- and metaphase-tetrads. But as shown above, precisely the same appearance of a two-strand chiasma is given by a process in which no torsion need be involved. Both Wenrich and Robertson have urged this fact against Janssens's interpretation; and I am fully in agreement with them so far as the later stages of meiosis are concerned. It may nevertheless be pointed out that both these observers have figured stages

[6] '19, pp. 101–104.

which at least suggest a process of torsion or strepsinema-formation in the early diplotene prior to, or very early during, the definitive opening out of the prophase-figures—*e. g.,* in Wenrich ('16), Fig. 75, or ('17), Fig. 23, and in Robertson ('16), Figs. 149, *a* and *b*. The case seems, therefore, by no means closed; and we may await the publication of Janssens's new results in greater detail, in the hope that more definite evidence may now be produced concerning the critical point at issue.

My own doubts on this matter first grew out of observations on the origin of the double crosses, which, as above indicated, involve a similar question concerning the chiasmatype. Janssens's earlier interpretation of the double cross, which I believe he was the first to offer, was in principle the same as that briefly indicated above and schematically shown in Figs. 5, III and 6 *D–E*. Later this interpretation became the prevalent one but was abandoned by Janssens himself ('09, '19) in favor of one which assumes a process of chiasmatype to be involved in the cross-formation. This interpretation starts with a comparison of the double cross to the region at which two rings join; and this is obviously correct under any theory (cf. Figs. 3 *D* and 6 *C, F*). Janssens, however, assumes the relation between the synaptic mates to be essentially as shown in the diagram here reproduced as Fig. 6 *A–B,* the two synaptic mates being bent at right angles, and united by their apices to form a cross which then splits straight through all four arms, thus giving two cross-over chromatids out of four. I seriously considered this interpretation in my own studies on the double crosses of Hemiptera, but finally became convinced ('12 and subsequently) that it does not correspond with the facts. More recently Robertson, Wenrich and Mohr have demonstrated the same conclusion in a very circumstantial and convincing manner in case of the double crosses of Orthoptera, tracing their origin step by step from the original diplotene in the manner indicated in Fig. 5, III. According to all these observa-

tions there is nothing in the history of these crosses, as thus far made known, to suggest an earlier process of torsion, chiasma-formation, and recombination. They indicate rather that the cleavage of such a tetrad straight through its two clefts involves simply one reduction-division and one equation-division (Fig. 6 *D–E*).

Robertson has pointed out that many of those appearances in the prophase- and metaphase-tetrads on which Janssens's theory was originally based are susceptible of a much simpler explanation than is offered by the chiasmatype-theory, namely, that they are a result of "misfortune in the prophase," due to secondary displacements of torsions at this time. Experiments with clay models have convinced me that this point is well taken, in respect to some at least of these appearances. It should also be clear from the foregoing discussion that conditions resulting from the persistence of the so-called two-strand chiasma in the metaphase-figures are readily explicable without the assumption of an earlier process of chiasmatypy.

In this brief review and critique of the cytological aspects of the question, I have not intended to take up an attitude of opposition towards the chaismatype-theory considered as an explanatory principle in genetics. On the contrary, I am not able to escape the conviction that somewhere in the course of meiosis some such process must take place as is postulated by Janssens and by Morgan and his co-workers, though I must admit that this opinion rests less on cytological evidence than on genetic. I have wished only to discuss the possibilities of the existing cytological situation and to offer a counsel of caution in respect to the chiasmatype-theory in so far as it is based on conditions seen in the later stages of meiosis. This means no lack of appreciation for Janssens's brilliant and fruitful work, which has opened up so remarkable a new field of inquiry. But a theory of such fundamental importance calls for critical treatment, and on its

purely cytological side too much has sometimes been taken for granted by writers on genetics. It is, I think, highly probable that the cytological mechanism of crossing-over must be sought in some process of torsion and recombination in the earlier stages of meiosis—perhaps during the synaptic phase of slightly later—and that this process may leave no visible trace in the resulting spireme-threads. To accept this, of course, would mean that such conventionalized diagrams as those here offered (Figs. 3, 5, etc.) should be so modified as to indicate exchanges which have earlier taken place between the synaptic mates. It must be said, on the other hand, that the actual evidence of torsion during the process of parasynapsis is still very inadequate and receives no support from some of the most careful recent work. One can not avoid a suspicion that some internal process of torsion (or of rotation, as conjectured by Correns) may take place in the early pachytene before the duality of the diplotene becomes externally visible. Conjecture concerning all this will however be less fruitful than further cytological analysis. The truth is that for the time being genetic development of the chromosome-theory has far outrun the cytological. We are in no position to predict when the plodding progress of cytology may be able to close the gap: nevertheless we have every reason to hope that the physical mechanism of the recombination-phenomena may in the end prove to be accessible to decisive cytological demonstration.

## The Spiral Looping of the Chromosomes and the Theory of Crossing Over

T. H. MORGAN

In his two recent papers Janssens calls attention to certain details relating to the application of the findings of cytology to the interchanges between homologous sets of linked genes. The first paper is a restatement of the situation as it is generally understood to-day, and calls

for no special comment. It ends with the significant statement

> At our next meeting I shall point out that the theory of the chiasma-type allows for an interpretation somewhat different from the view of simple splitting of the threads in a single plane that passes through the axis of the entwined threads.

Concerning the point here raised by Janssens I should like to add that the "simple interpretation" was given mainly to escape the somewhat complicated scheme involved in Janssens's theory. In this way it was hoped to avoid a too detailed account of the process that calls for pictures not readily understood except by cytologists familiar with the changes that take place when the twisted threads shorten and move apart. Unfortunately the very simplicity of the statement led one critic to infer that the interpretation must be wrong because at the nodal points the plane of the split appeared as though it cut obliquely through each chromosome itself. To avoid this I represented in later diagrams the chromosomes as made up of beads, and in this way tried to show that at the node each bead and its allelomorph are not divided, but go each to a pole. Even this diagram may prove too simple; for, if at the time of twisting each thread is also split lengthwise into two strands it is possible that only two of the strands fuse at each node. In Janssens's scheme to be described below this secondary doubling of each thread is seen to be an important factor in the situation.

Janssens states that the matter is not simple:

> The loops (Fig. 1 *B*) and the half loops (Fig. 1 *C*) that produce the chiasma lead to profound modifications in the twisted threads. These modifications are already indicated in the prophases, but they only become evident in proportion as the dyads ripen and prepare to place themselves on the spindle. We can not describe this here, but let us state nevertheless that the chiasma segments are placed in planes perpendicular to the segments adjacent to them as indicated in diagram II, Fig. 1. Once this fact is clearly seen it is not essential to add much to Morgan's phrase, since it expresses what really takes place. It need only be said: (1) In both maturation divisions a cleavage takes place

only in the equatorial plane of the figure. The first of these cleavages is here indicated by a dotted line in Fig. 1 *A*. (2) Moreover this plane produces a longitudinal cleavage of the chromosome and hence is equatorial in each of the alternating chromosome segments (rings) that lie exactly at the equator of the spindle of the figure (like that which occurs at a gonial mitosis), Fig. 1 *A* and *B*. (3) Finally, since the two spindles of the two maturation divisions that follow rapidly are perpendicular to each other, one may further add that each dyad will be split during the maturation (maiotiques) division by two planes at right angles to each other. At the first division, the equatorial division plane is perpendicular to the axis of the heterotypic spindle and during the second division the plane is in space, parallel to the original axis of the same spindle.

Janssens suggests the following considerations that have an application to Mendel's laws.

Neighboring segments pass easily into the same chromosomes when the direction of the twist is constant. When a segment is long it may be considered as carrying a longitudinal series of qualities, in conformity with the ideas held by Morgan. On the other hand the qualities supposed to be carried by the chromosomal segments are distributed amongst the germ-cells as though they were carried by chromosomes really independent confirming the law of disjunction of the characters in the gametes (Mendel).[7]

Let us return to a further consideration of the diagrams that have been published to represent the methods of crossing-over. In Janssens's scheme, Fig. 1 *A*, four complete rings are represented and the division plane appears to cut through each node, although the important details of how this is done are not shown in the figure, but may perhaps be inferred from Fig. 1 *C*, where the four vertical strands show what is supposed to have taken place. Crossing-over is represented as having occurred at four nodes. In *Drosophila* the genetic evi-

[7] In this sentence Janssens seems to imply that his chiasma theory explains "free assortment" between genes in homologous pairs of chromosomes, but obviously if the genes are in linear order, great numbers of them will go over together in the segments between the nodes, or on each side of a node. Hence the phenomena of linkage that places a very great restriction on Mendel's second law of assortment. It is this feature that we have always regarded as of the utmost significance in our theory of crossing over. It is obviously implied in Janssen's chiasma theory also, and I can not but believe that Janssens must intend to apply his theory in the same way in which we have applied our theory.

dence shows that as much crossing over as this does not usually occur. In our diagrams (Heredity and Sex, 1913), therefore, we represent only one or two real interchanges between the members of a pair of chromosomes because the genetic evidence shows, as stated, that, in the great majority of cases, this is what takes place.

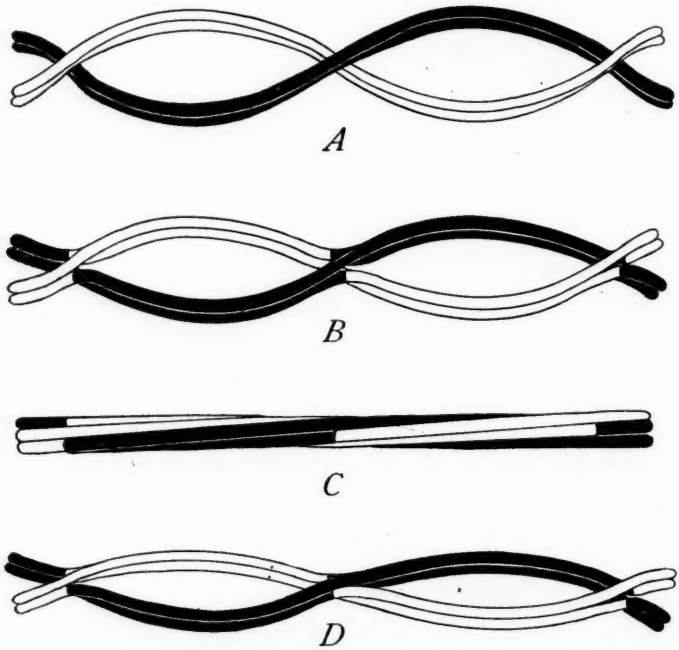


FIG. 7. Diagram of the looping of a pair of chromosomes that are already split lengthwise. *A*, two threads making one complete twist; *B*, the inner strands of each thread interchange at the crossing points; *C*, the threads next flatten against each other, still keeping their twisted configuration; *D*, just before, or after the conjugated thread enters the spindle it opens out by a reduction split that takes place in each segment of the thread. If the strands still keep their spiral relation, two strands cross over at each node; at the ends it is the non cross-over strands that cross, in the figure, but it is the other strands in each case that have broken and "crossed over." The crossed strands in the figure are not due to perspective.

The rings in two planes, as represented in Janssens's diagram, call for further analysis. We may call these rings *Bb, Cc, Dd, Ee* (Fig. 1 *A*). It will be observed that

in ring *Bb* the dark double thread (half ring) at the right separates from the light double half at the left. This is a reduction division for this segment. On the other hand in the ring *Cc* the division plane separates equationally the halves of the dark and of the light half rings. Crossing over takes place at the node between ring *Bb* and *Cc*, and at the node between the rings *Cc* and *Dd* there is another crossing over between the other two strands. Generalizing the result it may be said that crossing over of two of the strands takes place at each node. In the second division, that is supposed to take place here in the plane of the paper, there is assumed to be no further crossing over in either of the halves that have resulted from the first division.

Janssens points out that on this new scheme there is only half as much crossing over as on the scheme represented in our older diagram (1913); but it is obvious that this is only because in the latter whole chromosomes (each potentially or actually made up of two strands) are represented as crossing over at each node. If, however, we compare this latest scheme of Janssens with the figures that we have now recently published ("Physical Basis of Heredity," 1919) in which, following some of Janssens's earlier diagrams only two of the strands cross over at each node, it is perfectly clear that these later schemes of ours give the same number of crossovers per complete twist as do Janssens's present diagrams.

It may, therefore, not be without interest to compare Janssens's latest scheme with the one I have recently suggested in my book on the "Physical Basis of Heredity" (p. 105) where a figure is given that suggests an explanation of the opening out of a twisted conjugated thread in rings that lie in different planes. This figure is here reproduced, Fig. 8 *A–D*, modified only so far as to make it comparable with Janssens's new diagram. In *A* the two split threads are represented as looping or overlapping in an open spiral (an earlier stage than

Janssens's first figure). At this stage where the inner strands come into contact they are represented as fusing with each other at three nodes. The threads may next be supposed to flatten against each other to make the conjugated threads keep their spiral configuration and then condense to make the thick threads. In this condition they pass to the equator of the spindle or they may begin to open out before they reach the equator, Fig. 7 *B*.

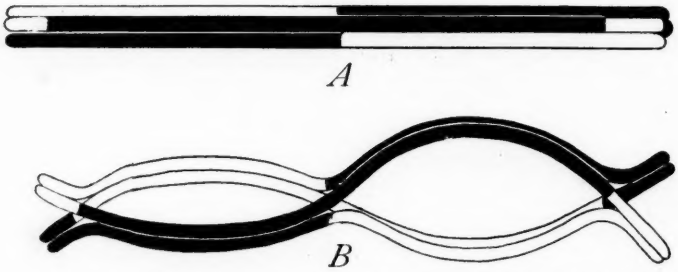


FIG. 8. Diagram showing how the twisted strands of Fig. 8, *C*, become straightened out (untwisted) as the thread shortens, so that the former spiral relation is lost. The resulting relation of the threads when they open out by the reductional separation is shown in *B*. *A*, this figure shows the relation of the strands when the spiral in Fig. 8, *C*, untwists, *i.e.*, as the thread shortens; *B*, if the thread shown in *A* now opens out by a reductional separation in each segment, the resulting figure, *B*, is the same as that of Janssens. In the middle of the figure it appears as though two "cross over" strands were crossing. This is here due to perspective.

If the first division is reductional for every part of the thread, the halves of the thread move apart in opposite directions, and as a consequence of the way the twisted threads have flattened against each other this opening out may produce rings lying in different planes, Fig. 7 *D*, not necessarily at right angles to each other, but at an angle with each other.

The rings are assumed to be due to the reductional separation of the segments of the chromosomes along the tetrad, but the further movements of the daughter chromosomes after they have reached the equator of the spindle must be referred to another mechanism that now comes into play, namely, the forces that carry the chromosomes to the poles. Under these circumstances the

threads may be thought of as separating without assuming such a strictly symmetrical form as Janssens's new diagram indicates, or in other words the separation of the chromosomes may take place as Janssens described it in *Batracoseps*. The suggestion that I made to account for the appearance of rings in different planes was made to meet an objection raised by Robertson and by Wenrich, namely, that the crossed threads (the chiasma threads) do not mean that crossing over has taken place in that region. They point out that the crossed threads may mean no more than that a *not-twisted* tetrad has opened out in different planes in consecutive regions. This obviously may be the interpretation of the crossed threads, but if as I suggested the opening out of the rings themselves in different planes represents consistently a reductional separation in a formerly *twisted thread,* then the cross threads come to have a meaning, for they represent the level at which an earlier fusion and reunion of the inner strands of the four strand stage took place. From this point of view the cross strands, while having nothing to do *at this time* with crossing over, nevertheless correspond to levels at which that process occurred.

I do not wish to appear to be advocating the scheme that I suggested as the best or as the only one that is involved in crossing over. Any scheme that accounts by means of twisting threads for interchange between the segments of homologous chromosomes will fulfill sufficiently the present requirements of crossing over. Much more cytological and genetic work too will be necessary before it is possible to state when and how this process goes on. One point alone seems at present to be indicated with some probability by the genetic evidence, namely, that it would appear simpler for the interchange to take place when the lines of genes are extended to the fullest extent possible, and this would seem most easily to take place, in the accurate way indicated by the genetic facts, when the leptotene threads have spun out to their farthest extent. Whether Janssens also ascribes to this

stage the essential step in the breaking and reunion of the strands remains to be seen when his new results are published.

Until Janssens publishes a full statement as to how he supposes the crossing over at the nodes to take place, whether at the time when the looping of the threads is present, or at an earlier stage, it is hazardous to make too detailed comparisons, but one relation should not pass unnoticed. In Janssens's figure four rings seem to be involved in one complete twist of the two chromosomes. In order to place these rings in such a position that a single (vertical) plane can sunder successive rings transversely and longitudinally in alternation, the rings must be turned so that two are exactly vertical and two are horizontal. A spiral relation of the threads can not be brought into this relation unless the threads first untwist. How this can be done is shown by a comparison of Fig. 7 with Fig. 8. In Fig 7 *A*, as explained, two chromosomes, each of two strands, are represented as looped around each other in an open spiral. In the middle of the spiral the two inner strands that touch are represented as fusing and reuniting to give the cross-over, and near the ends, where the threads cross again, the other two strands fuse, break, and reunite to cross over, Fig. 7 *B*. The threads are then represented as flattening against each other, still keeping their spiral configuration. When they open out again, by a reductional separation of the segments, Fig. 7 *D*, the rings are formed, and if the threads are still represented as keeping their spiral configuration no single plane, as explained, will separate them without cutting some of the strands. But if when stage *C* is reached in Fig. 7 the threads straighten out as they condense (*i. e.*, if they untwist) the result will be that shown in Fig. 8 *A*. If now the threads open out by a reduction division in each segment, the resulting figure will be like that shown in Fig. 8 *B*. This figure is the same as that of Janssens, and the halves can be separated in one plane, as he explains. We may conclude then, if the con-

jugated threads after crossing over do not untwist, they will give figures like those in Fig. 7 *D*, and such threads must be pulled apart as Janssens has explained for *Batracoseps*; but if after crossing over the twist is rectified as in Fig. 8 *A* the threads can separate as Janssens explains for the grasshoppers. In both cases the crossing over is represented as the result of twisting threads, and if such loops tend to have a modal length, the mechanism furnishes a beautiful explanation of interference which is one of the crucial tests to which our explanation of crossing over has been put.

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# VARIATIONS IN THE SECONDARY SEXUAL CHARACTERS OF THE FIDDLER CRAB

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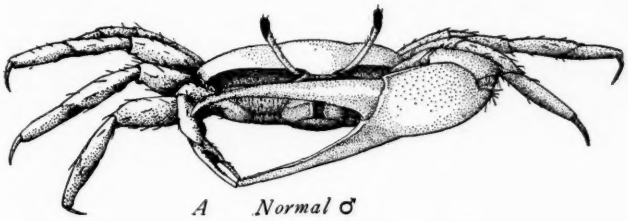
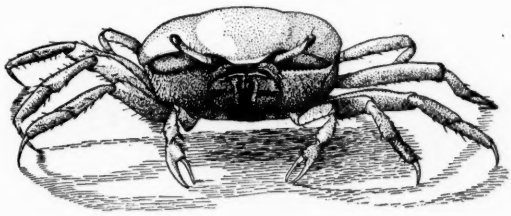
IN species in which the ordinary individuals are sharply separated into males and females there are occasionally found abnormal individuals in which characteristics of one sex are mixed with those of the other sex. We are only at the beginning of the study of these cases, but enough work has been done to make it more than probable that there are several, or even many different kinds of situations that call for separate treatment. That this is generally becoming recognized is evident from the different names that have been used in describing these cases, such as intersexes, sex intergrades, hermaphrodites, gynanders, androgynes, pseudo-hermaphrodites, free martins, eunuchoids, protandrous hermaphrodites; monœcious, diœcious, triœcious plants, indifferent larvæ, neuter insects, etc. It seems to me not worth while at present to attempt to classify such material until we have learned more about it. Whether all or only some of the aberrant types of fiddler crabs here described should be called intersexes depends largely on the definition of what that term includes.

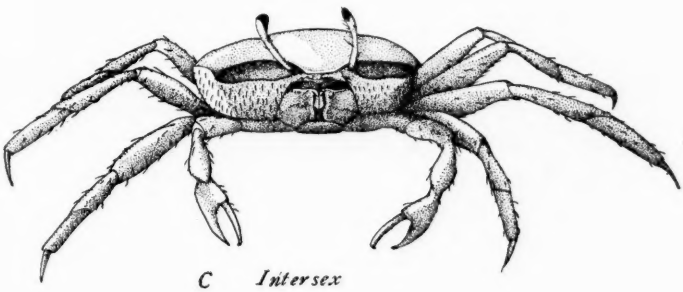
In the fiddler crabs the male (Fig. 1 *A*) and the female (Fig. 1 *B*) show not only the characteristic differences of other decapods, but one of the claws of the male is enormously enlarged. It may be either the right or the left one. If removed a new claw of the same kind regenerates from the stump although it may take more than one molt for the claw to become as large as the one removed. In the fiddler "compensatory regulation" does not take place as in some other decapods (Alpheus); that is, after removal of the large claw, the smaller one does not enlarge and substitute for it at the next molt.



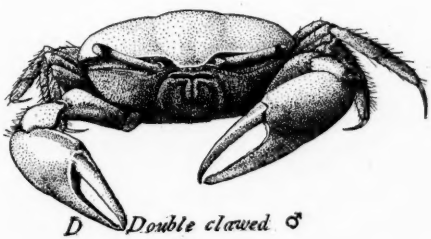
*A Normal* ♂



*B Normal* ♀



*C Intersex*



*D Double clawed* ♂

*Fig* 1

Moreover, and this is important, the characteristics of the new big claw are apparent as soon as the regenerated part begins to take shape, and even long before the molt.

The other most characteristic difference in the external parts between the male and the female is found in the abdomen. In the male, Fig. 2 *B*, it is narrow, in the

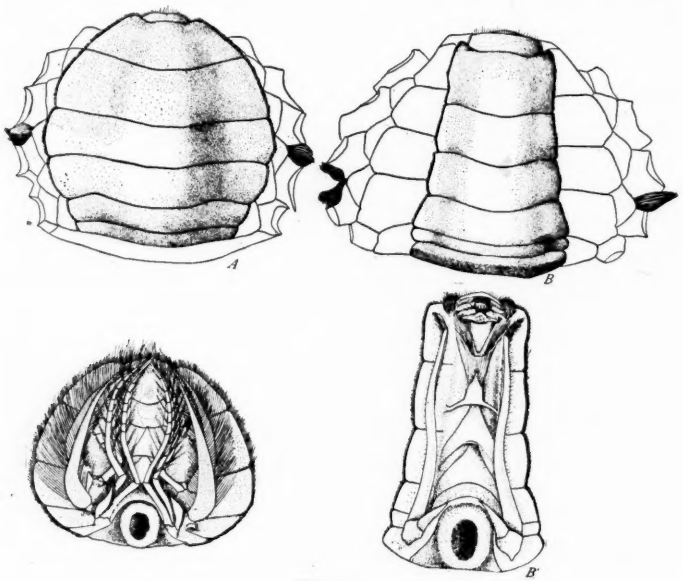


*Fig 2*

female, Fig. 2 *A*, it is almost as broad as the ventral surface of the thorax against which it is plastered. If the abdomen of the male is lifted up, its anterior pair of abdominal appendages, modified into copulatory organs, can be seen (Fig. 2 *B'* and Fig. 3 *A*). In the female the abdominal appendages (Fig. 2 *A'* and Fig. 3 *B*, *B'*) are entirely different, and are used to carry the eggs. The external genital pores can also be seen when the abdomen is lifted up; those in the male on each side of the middle line are in the segment that carries the last (5th) pair

of legs, in the female they are further forward on the segment that carries the third pair of legs.

In the summer of 1917, at Woods Hole, Miss Grace Hays, while sorting out some fiddlers, found an individual that had a small first pair of legs like those in the female, but an abdomen like that in the male. Another collection of crabs was made and three other such individuals were found. In the summer of 1919 the collectors at Woods Hole brought to me more fiddlers, and from them more aberrant forms were obtained. It then

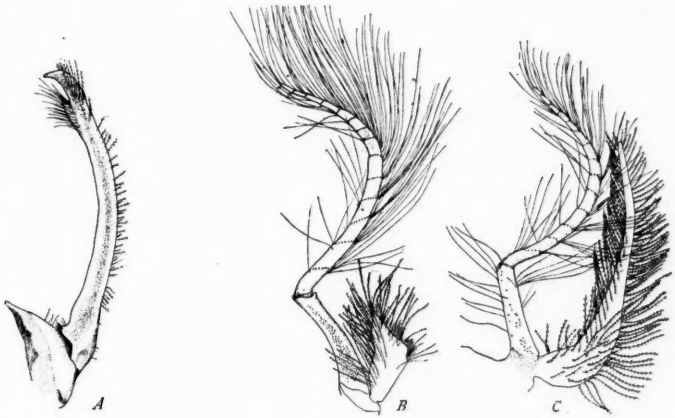



*Fig. 3*

seemed worth while to find out how often such individuals occur in this locality. Thanks to the interest shown by Mr. Wm. Procter and Mr. Alfred F. Huettner a large number of crabs were collected and carefully looked over.[1] As shown in the following table the number of aberrant individuals was found to be about .0077 per cent.

| Normal | "Intersex" | |
|---|---|---|
| 353 ..... | 5 | June 24, 1919 |
| 50 ..... | 2 | 28 |
| 1,245 ..... | 6 | 30 |
| Total 1,648 ..... | 13 | |

[1] A few small intersexes were later obtained by Mr. Lionel Strong at Cold Spring Harbor, L. I. Mr. Procter later collected 2,068 crabs at South Wellfleet (July 4), but found no aberrant individuals amongst them.

A cursory examination showed that two types of individuals were present. The larger individuals had the abdomen of the male sex, but both claws were small and

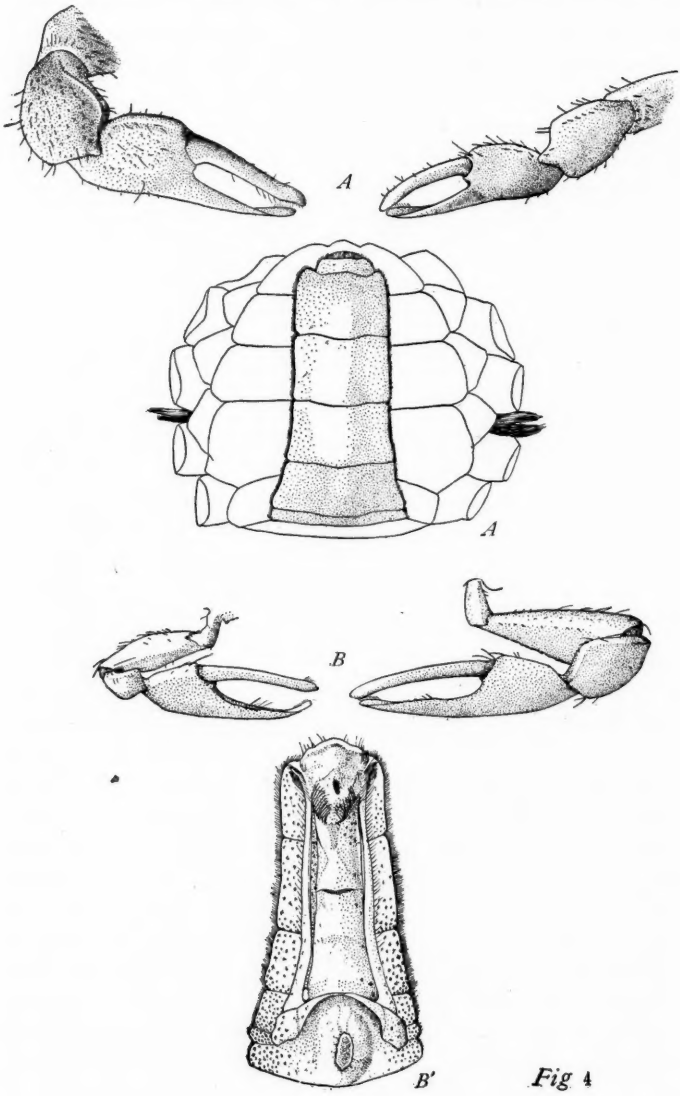



*Fig* 4

more like those of the female (Fig. 1 *C*). The other individuals had abdomens not quite so broad as those of typical females of the same size, Fig. 4 *B'*, yet their claws were generally small, like those of the female, and showed no indications of a variation towards the male type. Since the younger stages of some crabs, such as the blue crab, have a narrower abdomen than that of the adult female until the last molt, it seemed possible that these "intersexes" might at a later molt turn into typical females. They were kept therefore and well fed for two or three months during which time they molted once, Fig. 4 *B''*, or even twice. A comparison of the old skin showed that the condition of the abdomen and claws had not changed. It is evident that this condition can not be explained as transitory. Nor is it juvenile because normal individuals of the same size have the abdomen full width.

A more detailed examination of these two types may now be given. The most striking fact is that all of the full grown crabs belong to one category, and all of the smaller ones to another. The former of which there are six, have a strictly male abdomen regardless of the condition of their claws, and what is more significant the external genital pores are at the base of the last pair of legs, as in the normal male. As shown in Fig. 2 *A'* and *B'*, the abdomen is exactly like that of the male. On its inner side it contains the two long copulatory appendages of the male. The chelæ in three individuals are small, Fig. 4 *B*, and of the same size, resembling those of the female. In the other three one of the claws is somewhat larger, Fig. 4 *A*, than the other and shows unmistakably evidence of variation toward the male. The genital pores are, as stated, in the same position as in the normal male, and there are no indications of female pores further forward. In two cases at least, the crabs molted, but did not change their characters. In the second group, Figs. *A*, *B*, *C*, *D*, there are sixteen individuals. There is amongst these no obvious relation between the size of the

crab and the relative width of the abdomen. Some of the smallest have the narrowest abdomen. There is some correlation between the character of the abdominal appendages, particularly the first pair and the width of the abdomen. As shown in Fig. 6 *A, B,* this appendage does not appear as much like that of the female of the same size, Fig. 6 *C,* as would be expected were it strictly female, yet it can not be said to be male-like, and the narrowness of the abdomen may be responsible for the difference.

The claws are like those of the female in all cases.

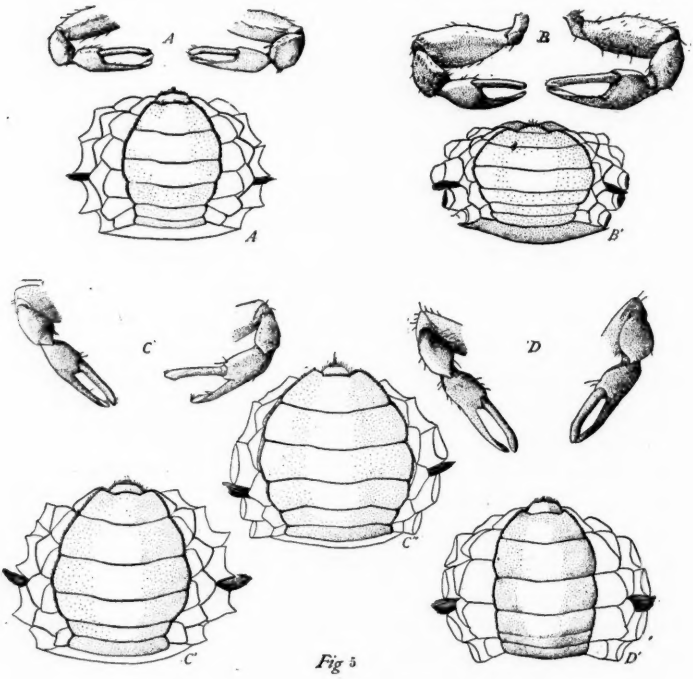



Fig 5

After the foregoing account was written I have received from Miss Rathburn a number of fiddler crabs, exactly like those recorded above, from the collection in the National Museum in Washington. They fall into the same

two groups. One large male, labelled *Uca pugilator* (18286), has a pair of small female like claws. It comes from Northampton Co., Va. (1894). It belongs to a different species from those described above.

There are in this collection eight small female-like crabs with the abdomen narrower than that of the normal female of the same size. All of them have both small claws of the same size. In those with the narrowest ab-

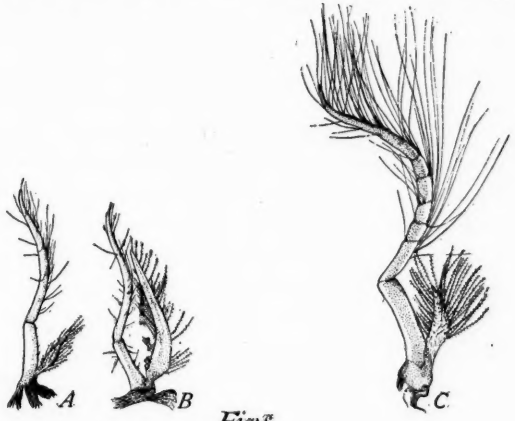



Fig. 6

domen, the abdominal appendages are straighter and less plumose than are those of the normal female of the same size. This condition might be described either as a juvenile, or as a less female-like condition, but not necessarily more male-like. In size and shape the abdomens of these crabs are like those of Fig. 5 *A, B, C, D.* In addition there is one small individual (17688) labelled "pugilator," with the abdomen about half the width of a normal female of the same size of the other species.

There is also one further variation in the fiddler that is different from the preceding ones. It is shown in Fig. 1 *D.* Mr. G. M. Gray found this male fiddler (*Uca pugilatur*), and with his permission I am able to figure it here. It had two large claws, both like the claw of the normal male. I find that Professor S. I. Smith, of New Haven, recorded in 1869 a similar case of *Uca pugnax.*

At present we are entirely ignorant as to what causes determine in the normal male that only one side develops a big claw. The asymmetry of the fiddler appears to be analogous to that of the asymmetry of snails and of the one-sided operculum of certain annelids (*Hydroides*), etc. It is generally supposed that something comes in during the development of the male crab that turns the scale one way or the other; and once determined the relation persists during life in fiddler crabs, although in other decapods, as shown by Przibram, the initial difference may be reversed during regeneration if the large claw is removed and the small one left. Until we get further information concerning these matters it would be idle to speculate as to what has led in this male to two large claws.

It is interesting to note in the case of this male with two large claws that it differs from the ordinary males by doubling the kind of difference that distinguishes the normal male from the female. It can scarcely be said to be an inter-sex, for the difference is not in the direction of the opposite sex, but away from it. If some designation is called for, it might be said to be a super-male, or at least an over-clawed male.

## DISCUSSION OF THE RESULTS

If we compare the results of parasitic castration of certain decapods with the conditions described here in the fiddler crab several resemblances and differences become apparent. First in none of the cases of parasitized crabs are the external genital openings affected. They furnish a certain clue to the original sex of the individual. Likewise in the large fiddlers the male external genital pores are present, and there are no female pores. The individuals have probably always been males. Whether the condition of their claws is due to some disease, or possibly to some internal parasite, or to a change in the genetic complex, can not be stated. It is even possible that it may be due to none of these, but to some "accident" in the development, *i. e.*, to some change in the em-

bryology that determines the asymmetry of the normal male. The occurrence of the male with the two large claws may seem to favor the last interpretation; for here we find the reverse relation and it does not seem probable that such an over-clawed male could have arisen through parasitism, or through disease, although the argument for a genetic change can not be entirely set aside.

In regard to the other group containing the small aberrant forms the situation is somewhat different. All of these have started as females, as the location of the external genital pores clearly indicates. Yet some of them show also an apparent change towards maleness by the narrowing of the abdomen or possibly a retention of the juvenile condition. Here the change, if it be a change, is in the reverse direction from that shown by most of the intersexes described by Giard and by Geoffrey Smith, since starting as a female the change is towards maleness, while in the parasitized crabs it is the female that changes towards the male. The different degrees to which the change has taken place in different individuals may seem to indicate disease or parasitism. The absence of further change in the same direction in the next or following molts is not perhaps so favorable to this interpretation. But on the other hand the absence of adult crabs of this sort, or at least their infrequency may mean that these individuals do not reach maturity, and may therefore be diseased or infected[2] or that in the adult the full-sized abdomen is attained. These questions must be further investigated before a decision can be reached.

## General and Hypothetical

It may seem, as stated above, that some of the changes seen in the fiddlers may be similar in kind to some of those brought about in other crabs by becoming parasitized. Giard has described several cases in crabs and

[2] Geoffrey Smith has described changes in the crab *Inarchus* brought about by inflection of a gregarine. The abdomen and claws of the male were changed in much the same way as when this crab is parasitized by a barnacle. Giard has described an hermaphrodite amphiurian, parasitized by Orthenectidæ, that cause the ovary to degenerate while the testes continue to function.

other Decapods parasitized by other crustataceans (*Sacculina Portunion, Peltogaster,* etc.), in which changes take place in certain parts of the body that approach the condition found in the opposite sex. These changes involve most often the abdomen and its appendages, and in one species at least the claws. The most marked changes involved the male, producing in him alterations in the direction of the female. In one case *a female* is described as showing some effects of the parasite but if I am correct Giard interpreted this change as resulting from the retention of the juvenile condition. Giard contrasts the changes in the male crabs with those produced by castration in the vertebrates. He seems to imply at times that he supposed the effects are produced by the loss of the gonads. At other times, however, he speaks definitely of the changes as some sort of symbiotic relation between the host and the parasite—an idea similar in many respects to the later and more elaborated hypothesis of Geoffrey Smith. In fact, in summing up the evidence Giard recognizes two classes of cases; those due to the indirect action of the parasite by way of the testes, and those due to the direct, by action on the host. It was, of course, at that time natural to suppose that in both groups, vertebrates and crustaceans, castration acts in the same way, especially as the case of the vertebrates had been long in the literature, and zoologists had become familiar with this kind of effect. Moreover at the time other evidence was lacking to show in other groups that the gonads have no influence on the development of the secondary sexual characters. But the work of Oudemanns that was later fully confirmed and extended by Kopec and by Meisenheimer and by Kellog removed any prejudice that the situation in the vertebrates had brought about, so that at the time when Geoffrey Smith wrote the field was clear for an independent judgment. As stated Geoffrey Smith brought forward evidence that seemed to him to show that the changes in the secondary sexual characters in parasitized males were due to physio-

logical processes set up by the parasite in the host. He even went so far as to compare directly and in detail the substances called forth in the host by the action of the parasite. Without discussing these questions here (since I have recently discussed them in my paper on "The Genetic and Operative Evidence Relating to Secondary Sexual Characters," Carnegie Publication No. 285, 1919) it is evident that crucial experiments must be made on the crabs themselves before a conclusive case can be made out. This is by no means a simple matter as I have found. During the last three summers at Woods Hole I have tried to carry out experiments on crabs to test some of these questions. All attempts to remove the gonads in fiddler crabs have failed, because of the delicacy and distribution of the organs, and the fatalities that result when the carapace is lifted up. Attempts such as Stamati made in 1880 to destroy or injure the gonads by injecting substances through the genital pores have also failed, because of the delicacy of the tubes and the distance of the gonad, in the male, from the external genital opening.

Some important observations made by Kornhauser (1919) on the effects of parasitism of the tree-hopper, *Thelia bimaculata,* by the hymenopteron, *Amphelopus thelia,* have a bearing on the preceding discussion. The egg of the parasite is deposited within the body of the nymph of *Thelia* from the first to the fifth instar. The egg or eggs give rise to a number of "polyembryonic" larvæ, that ultimately destroy the host. Infected males show in the adult stages many of the characteristics of the female, the degree to which the change takes place being mainly dependent on the stage at which parasitism occurred. The change involves the pigmentation, the size, certain abdominal spines, the shape of the abdominal sclerites that approach or even reach the condition found in the female. The genital appendages do not change into those of the female, but remain small and lose their specific characteristics.

Parasitized females do not assume any of the features peculiar to the males.

The gonads in both sexes usually degenerate, and an accumulation of fat takes place in the abdomen of the host. Two exceptional cases have an important bearing on the cause of the changes resulting from the parasitism. One male was found that had been parasitized, and although it had been considerably changed towards the female in its somatic characters it "contained full-sized normal testes with many spermatozoa." Evidently then the changes caused by the parasite are not due directly to the destruction of the gonads as shown by this individual in which the gonads had escaped. This accords with the results of artificial castration in other insects.

The other exceptional case (fourth instar) had a "perfect female soma" but contained testes. The individual had started as a female. There was evidence of this, though it is not conclusive, in the chromosome counts of the somatic cells. It must be supposed that at an early stage something changed the cells of the germ-track, so that its cells developed into testes. This conclusion is borne out by a count of the chromosomes of the testes that show 21 cells in the spermatogonia, one of them being the large X chromosome characteristic of the male. An early "elimination" (loss) of an X chromosome from the mother cell of the germ-track, such as occurs in *Drosophila,* would seem to be the simplest explanation of this case, as suggested by Kornhauser.

The conclusion from the evidence is quite convincing, namely, that the several characters peculiar to the male are changed into those peculiar to the female as a result of the direct action of the parasite, and not through any influence by way of the gonad.

### FEEDING FIDDLER CRABS ON THE GENITAL GLANDS OF THE OPPOSITE SEX

During the summer of 1918 I carried out some feeding experiments. The occurrence of hormones in the repro-

ductive "glands" in other animals suggested the possibility that the secondary sexual characters of fiddler crabs might be affected if the crabs were fed on the organs of the opposite sex during the period of regeneration of the large claw. Male fiddlers whose large claw had been previously removed, were fed exclusively, and at intervals of two or three days, on the ovaries of female spider crabs. The fiddlers were kept until they moulted about a month or two later. The new claw showed all the characteristic features of the normal large claw. Its regeneration had not been affected by the character of the food.

Female fiddlers, one of whose claws had been previously removed, were fed on the testes and the ducts leading from them of the male spider crab. Other females were fed on what appears to be a large gland in the posterior part of the abdomen of the male. No effect on the regenerating claws were observed.

These negative results do not show that there is no hormone in the gonads of the crab that affects the secondary sexual characters, for even if there were such, it might not be able to produce its effect through the digestive tract. Only positive results of this kind would be important but none were obtained. As the results were entirely negative they need not be further described.

A more promising test consisted in boring a hole in the carapace of the male fiddler and inserting pieces of the ovary of the female fiddler. Conversely for the female. There are certain implications in Geoffrey Smith's views that seem to imply that male tissue can not survive and grow in an individual with female metabolism, and perhaps conversely for the male. The small grafted pieces often become lost, and it is difficult to determine later by means of sections how far the tissues degenerate and how far they become implanted and grow. I have not had the time to carry out a detailed study of the sections, but they seem worthy of further examination. No effect on the claws were produced.

### A PIECE OF AN OVARY PRESENT IN A MALE CRAB

A normal male fiddler was opened to obtain pieces of its testis. In the region where the left testis is supposed to end there was found a small piece of ovary with its purple eggs. These were sectioned and found to be normal eggs. This observation is significant in so far as it shows that ovarian tissue can grow and differentiate in a purely male environment. The explanation of this occurrence is not at hand. One is tempted to refer to it an abnormal cell division in the testis of such a sort that the chromosome combination (if such exists) to produce eggs was formed, but in the complete absence of information concerning the chromosome composition of the male and female crustacea, such an attempt would appear premature.

### INTERSEXES AND GYNANDROMORPHS IN CRUSTACEA

If it does not seem probable that the aberrant types in the fiddlers, that have been described above, can be safely referred to parasitism, it may not be without interest to point out that there are many other queer cases of sex mixtures in the crustacea, that do not appear in any way connected with environmental changes—or at least not directly.

Many cases of intersexes have been described in the Cladocerans, in the genera *Daphnia, Alona, Leptodora, Simocephalus,* under the name of androgynes, gynandromorphs, intersexes, etc. (Kurz, 1873. Grochowki, 1896. Woltereck, 1908. Kutner, 1908. Ashworth, 1913. Agar, Banta, 1918. De la Vaulx, 1915 and 1918). The antennæ more often show modifications characteristic of both sexes, but other organs are frequently involved, including even the gonads. There are no indications of parasites in any of these cases, where owing to the transparency of the body they would be easily detected if present.

Kutner has recorded the sporadic occurrence of intermediate forms through 12 generations of *Daphnia pulex* —in a line having a relatively high percentage of these

forms. No recognized form of inheritance can be detected in these parthenogenetic lines. If, as generally supposed, there is no elimination of chromosomes in the parthenogenetic egg of Daphnians, the expectation would be that all offspring of an intermediate would be like the mother, whether the "character" were recessive or dominant. It would seem then that if certain lines of parthenogenetic Daphnians do produce more intermediate types than occur in the general population, we must look either to irregularity in the chromosome behavior or to environmental influence. The latter seems excluded by Banta's results to be mentioned later. The former can only be hypothetical until such differences are found. Nevertheless the discovery of such cases in other groups (*Drosophila, Œnothera*) makes the suggestion at least not so speculative as might have appeared several years ago.

The most important results are those recorded by Banta, not only because he has obtained a much higher percentage of intergrades, but because these appeared in a pedigreed strain, and the appearance of the intergrades has been carefully followed through later generations. In the 131st generation of one of the strains there appeared males, females and *sex intergrades.* The last group composed of "males with one or more female secondary sex characters, females with one to several male characters and some hermaphrodites with various combinations of male and female secondary sex characters." Highly male-like females produce only a few young or are sterile. "A female intergrade with as many as six strong male secondary characters rarely produces young." Males that have one or more female characters have nearly always incompletely formed testes. The strain was kept up by breeding from female intergrades that continued to produce females, males, and sex intergrades for 16 generations with no apparent change in the ratio of the various sex forms." The picture here presented can not but suggest some sort of disintegration or

variation in the chromosome mechanism. At present we do not know how a parthenogenetic female sometimes produces female (parthenogenetic) broods, at other times male broods or sexual eggs. That such changes may be brought on by environmental changes seems not improbable from the large amount of data already collected. The results in these respects are so similar to those in rotifers where the situation is now under control (Whitney) that one can scarcely resist the conviction that in both cases the environment acts in producing the changes. But while we have no explicit evidence, as yet, even in *Hydatina,* that the environment acts only by bringing about changes in the chromosome mechanism, there is at least nothing known opposed to such a view, and some general arguments that incline one to anticipate such a discovery. Until these matters are set straight not much is to be gained by speculating as to how the sex intergrades of *Simocephalus* and other *Daphnia* arise. But if it should be found that the normal cycle is caused by alterations in the chromosome cycle, as has been shown in fact for Phylloxerans and Aphids, then I think we may have to look to some aberrations in the same mechanism to explain these anomalous cases. Indeed the kind of inheritance described by Banta appears to be one that might be expected from such a situation.

In the genus *Cyclops,* Mrázek (1914) has described "androgynes" that have modifications in the antennæ, and Bremer (1914) has recorded two cases of "pseudohermaphrodites" in *Diaptomus.*

In sharp contrast to these kinds of intersexes in the lower crustaceans stand out the bilateral gynandromorphs that have been found in two genera of lobsters. Nichols in 1734 described a lobster whose right side was female and whose left side was male. Dissection showed an ovary in the female side and a testis on the left. A similar case was described for *Palinurus* in 1902 (Burger), but no dissection was made.

In the *Canadian Naturalist* for May, 1919 (Vol. XXXIII, No. 2), there is a description of another "hermaphrodite" lobster. In reply to a letter of inquiry that I sent to Mr. A. P. Wright, he states that the lobster was sent to him by Mr. Halkett and that the animal is male on the left side and female on the right side. There is an ovary on one side and a testis on the other. These three cases appear to differ from the preceding cases and suggest a direct comparison with the bilateral gynandromorphs of insects. It is quite possible that they owe their origin to some similar chromosome "elimination" in the course of development, but it should not be forgotten that sex-chromosomes have not been reported in the lobster, although the cytology of the spermatozoa has been often examined.

Another decapod, *Gebia major,* has been shown by Ishikawa to be hermaphroditic. The anterior end of the testes produces sperm and the posterior eggs. A pair of ducts leads from each part to the exterior. Such individuals appear to function only as males. Spitschakoff found in a crab, *Lysmata seticaudata,* that both ovaries and testes are present with their ducts and external genital pores on the third and fifth pairs of legs. The anterior end of the gonad functions as ovary and the posterior as testes, which is the reverse relation from that of *Gebia.*

In crayfish belonging to the genus *Parastacus,* von Martens, 1870, von Ihring, Faxon, 1898, and Lonnberg, 1898, have described genital pores on the third and fifth pairs of appendages. Lonnberg has dissected some of these individuals. He finds testes in some of them, ovaries in others, but in both cases there are two pairs of ducts lead to the genital pores on the third and fifth pairs of legs. Here there is no true hermaphroditism, but on the contrary separate sexes. Nevertheless the ducts characteristic of the males and females in other species with separate sexes are both present in all individuals of *Parastacus.*

Selbie points out that Wollebaek (1909) showed that *Calocaris macandreæ* is normally hermaphroditic, each individual having testes and ovaries. The first pair of abdominal appendages has its tip expanded in all individuals as in male decapods.

In some of the amphipod crustaceans, the occurrence of ova in young males seems to be a normal occurrence recalling the conditions in frogs. Nebeski (1880) stated that the anterior end of the testis of *Orchestia gammarillus* contained ova. DellaValle, 1893, never found many eggs in *Orchestia deshayesii,* and none at all in sexually mature males. Geoffrey Smith made some further observations and attempted to explain the results on his anabolism-metabolism view. Ch. Boulenger studied the two forms mentioned above. Out of 137 males of *O. gammarellus,* 135 had no ova and 2 had a few ova anteriorly. Of small individuals, on the other hand, nearly all contained ova in the testis (198 with and 19 without ova). "These results are therefore much at variance with those obtained by Smith and I am at a loss to explain how he arrived at his conclusions."

## INTERSEXES AND HYBRIDIZATION

In recent years several cases in which intersexes appeared in considerable numbers have been shown to be due to intercrossing. This raises the question whether some of the aberrant individuals here described may not have been due to crosses between the two species of fiddlers *Uca pugnax* and *Uca pugilator.* It is true that the latter is found most often in sandy stretches and the latter on muddy flats, yet the two are not infrequently found together or in nearby localities. The larger intersexes appear to be unmistakably *Uca pugnax*; the smaller are more difficult to identify. Miss Rathburn has examined both the large and the small individuals here de-

[3] Ewing ('85) has described a blue crab in which the abdomen is intermediate in width between that of the adult male and female. He thinks that the individual is hermaphrodite, but as shown by Churchill, the peculiarity described is the normal condition of the juvenile female before the last molt.

scribed and reports that they all belong to the species *Uca pugnax,* and show no signs of being hybrids.

The most interesting cases of intersexes are those produced by Goldschmidt in crosses between different races of the gypsy moth. He describes some crosses that give individuals showing only a slight tendency towards the opposite sex; other crosses go further until finally the male may be completely transformed into females, the change even including the appearance of eggs in the gonads. Conversely females may be changed towards maleness in various degrees depending on which varieties are crossed. His interpretation in general is that the two kinds of sex genes have different values in different races, so that the hybrids are in these respects betwixt and between so far as the influence of the sex genes is concerned. As I have recently discussed at some length Goldschmidt's view (see Carnegie publication, No. 278, 1919, and No. 285, 1919), I need not go over the ground again.

Harrison has more recently described intersexes in the offspring of different species of moths belonging to the family of Bistonidæ.

In this connection it is interesting to note that some of the phenomena seen in these moth crosses appear when crosses are made between two species of *Drosophila,* namely, *D. melanogaster* and *D. simulans.* Made one way the cross gives only females as A. M. Brown discovered, and as Sturtevant has verified. Reciprocally only males are produced, as I have found, with a few females hatching late in the series. In both cases, however, the hybrid males and females from the two crosses, although sterile, are strictly one or the other sex both in their gonads and in their secondary sexual characters, but as stated the gonads are rudimentary. Sturtevant's recent discovery of real intersexes in a race of *Drosophila simulans* has an important bearing on the interpretation of intersexes. He finds in a certain line that individuals appear that show characters both of the male and of the

female, including especially the genitalia. They have rudimentary gonads. Breeding from normal heterozygous sisters and brothers he has shown that there is present a recessive gene that gives the intersexes when present in double dose in females. This gene is in an autosome. The results are shown, therefore, not to be due to a change in the gene or genes for sex, but to a gene whose effects are superimposed on the influence of the sex genes. It is evident that such a possibility must be reckoned with in interpreting other cases.

Intersexes have been found in human lice, *Pediculus,* by Keblin and Nuttall. The evidence makes it probable that these arise most frequently when the body louse, *P. corporis,* crosses with the head louse *P. capitis.* These intersexes have both male and female gonads and genitalia in the same individual, differently combined.

It has long been known that crosses between Gallinaceous birds give rise to males that are sterile although such males are not described as intersexes. Whether only the male hybrids survive or whether the female hybrids are sometimes turned into males is not known. Guyer has raised the question as to whether the individuals in question if ever females might be classified as males, because of the rudimentary condition of the ovary. It is well known to-day that removal of the ovary of the hen causes her to assume the male plumage (Goodale), and also it is more than suspected that tumors in the ovary or other diseases of that organ produce a like effect on the plumage. But Guyer points out that in the few cases examined by him testes were present. Riddle has described many cases in hybrid doves in which the sexual behavior of certain individuals showed them to have opposite sex tendencies from that indicated by their gonads. These he calls sex intergrades. It is well known to poultrymen that birds in poor condition sometimes behave queerly in their sex relations. It is possible that the weakened condition of these doves may have something to do with their anomalous behavior. But aside

from this question it is possible to state that in one of the crosses at least, in which a sex-linked character is involved, there is good reason to believe that the normal sex chromosome relations persist. It is scarcely legitimate under these circumstances to suppose that the ordinary mechanism of sex production is changed in such cases in the sense implied or stated that males have been turned into females and females into males. Moreover it is sometimes overlooked that if such were the case very anomalous sex inheritance would follow were it possible to breed such hybrids. Unfortunately this is not possible in most of the cases at issue, since the hybrids are sterile, but in the few hybrids that have been bred no such disorder of the machinery appears and the individuals appear to be true to their sex. One must look, I think, in other directions for an explanation of the results.

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# THE SABLE VARIETIES OF MICE

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THE variations in darkness of certain forms of fancy mice have called forth different interpretations from the various investigators who have studied them. The present report is intended as a contribution of experimental data, treating these differences as graded variations.

The varieties of mice most commonly exhibiting differences in darkness comprise those races known as sables. Such mice are distinguished by a yellow belly and a back of some shade of black or brown with which yellow may or may not be mixed. They were first reported by Bateson in 1903 but Miss Durham (1911) was the first to breed them experimentally and to catalog the variations within the sable race. Little (1913) classed sables as yellows with varying amounts of dark pigment in the hairs on their dorsal and lateral surfaces. Dunn (1916) offered the explanation that all sable varieties differed from ordinary yellow by a factor or factors determining the quantitative increase of dark pigments, so that sables formed a continuous series of increasing dark dorsal pigmentation from clear yellow to black-and-tan in which the back was intense black while the yellow pigmentation was exhibited only on the belly. Onslow (1917) was "led to look upon sable as a pattern factor which could give a yellow belly to a mouse of any color," but he did not publish the experimental evidence upon which his conclusions were based. He criticized Dunn for further involving the nomenclature of the sables through the use of the names "black-and-tan," "brown and tan," "black sables," and "brown sables," to designate the members of the sable series.

The use of the above term is, I believe, justified because black-and-tan is recognized by the English fanciers as distinctly different from ordinary sable, and because none of the sables described by Miss Durham behaved as did

the mice used in my experiments. Miss Durham described "black, blue, chocolate and silver fawn mice which differ only from the ordinary forms by having yellow bellies," but they subsequently always moulted into ordinary sables which have a "dark black or brown streak down the middle of the dorsal region while the rest of the mouse is yellow." Black-and-tan however does not moult to ordinary sable. Even at the age of twenty months black-and-tan is entirely black except for the yellow belly and yellow ticking on flanks and muzzle. Since these mice were different from ordinary sables, they were given a name to indicate the difference. Moreover when they were crossed with various non-black-and-tan varieties there were produced in the second generation mice resembling the black-and-tan parent, others intermediate between black-and-tan and yellow, and conforming to Miss Durham's description of sable. The latter were called black sable or brown sable to indicate the color of their non-yellow pigment. I am in sympathy with Onslow's desire to prevent a duplication of terms but I believe that the names employed are required by the presence of types which differ both genetically and somatically.

Sooty yellows may likewise be included in the sable series since these mice appear when black-and-tans or sables are crossed with non-sable varieties. Sooties can not be distinguished simply as yellows which are heterozygous for black, for yellow mice which carry black may show no trace of sootiness. Factors additional to the black gamete are involved in the production of sooties and these factors are present not only in the sooties but in the blacks which they produce. Little (1916) used blacks derived from sooties in crosses with wild agouti and obtained agoutis which were much darker dorsally than any wild agoutis. I have obtained similar results from such crosses. Certain blacks with which yellows have been crossed to produce sooties evidently carry some of the factors for darkness which appear in greater concentration in sables and black-and-tan as well as in

the blacks derived from these varieties. Sooty, then, appears to be a lower stage of sable in the more complete restriction of non-yellow pigments from the hair.

In addition to the varieties treated above it is necessary to speak of light bellied mice which can not be included in the sable series. I refer to the light-bellied agouti variants reported by Cuénot and Morgan. These variations have been shown to belong to a series of multiple allelomorphs in which the other members are ordinary agouti, yellow, and non-agouti. The light-bellied agouti also arose spontaneously in Little's 1916 crosses between gray-bellied agouti and dilute brown. Such light-bellied agoutis bred true and when crossed with a non-agouti variety they produced in $F_2$ only light-bellied agoutis and normal non-agoutis. This result contrasts strongly with the result of a cross of black-and-tan with wild agouti which produces only sables and gray-bellied agoutis in $F_1$, while in $F_2$ there result yellows, sooties, sables, black-and-tans, agoutis and darkened agoutis. The difference is readily seen to be due to the yellow gamete of the sable series.

To explain the results of the genetic behavior of sables one is led to review the origin of the varieties concerned. The wild house mouse is undoubtedly the ancestral type from which all varieties of fancy mice have descended. Its pelage contains the three fundamental pigments of mice: yellow, black and brown, formed in the mosaic known as the agouti pattern by the presence of a specific gene "A." Each pigment is likewise determined by a gene, Y for yellow, B for black, b for brown (absence of black) and by loss of one or more of these genes, or by the gain of other genes determining the distribution of the pigments present, the whole array of fancy varieties has resulted.

Yellow was shown by Cuénot to be due to a change in the gene "A," resulting in the presence of a restrictive factor which limits the distribution and amount of black and brown pigment, the eyes alone being dark pigmented while black or brown pigments are present in the hair and

skin in such small amounts as to leave the pelage clear yellow. All three fundamental pigments are present in yellow and it is essentially an agouti in which the dark pigments are quantitatively restricted and reduced. This gene acts as the dominant allelomorph of agouti, light-bellied agouti, and non-agouti. Black mice, on the other hand, represent no quantitative reduction in amount of pigment but only the absence of the genes for yellow and agouti. The sables contain a gene allelomorphic to agouti and non-agouti. The evidence shows that this gene is common to yellow, sooty, sable and black-and-tan mice. This gene is a lethal. When it is present in both gametes uniting to form a zygote it causes the death of the zygote. This lethal gene (yellow) might conceivably assume several forms and cause the differences noted among the sable varieties. If such were the case, yellow and sable varieties would be members of a series of multiple allelomorphs of a single gene. Such series have been demonstrated in the gene for white eye in Drosophila by Morgan and his co-workers; in the color gene in the guinea pig by Wright (1915); and in the agouti gene in the mouse itself as quoted previously. But if the black-and-tan mouse or a sooty were due simply to a different form of the yellow gene the difference of their black recessives from ordinary blacks would still remain to be explained. Moreover yellow and the members of the sable series are more closely related to each other than as mere members of a multiple allelomorphic series. They do contain an identical gene, and unlike multiple allelomorphs can be changed one into the other more or less completely. Their difference rather inheres in their possession of modifying genes determining the quantitative increase of black or brown pigments not only in connection with the yellow gene itself but in connection with the genes for black, brown and agouti.

Such modifying genes can not be merely changes in a distributive gene such as agouti or the gene for restriction which causes yellow, for their presence has been demonstrated in non-agouti, non-yellow animals. They

must rather be related to the formative genes for black and brown pigment, so that the number of black and brown pigment granules is increased in proportion to the number of modifying genes present. I have examined microscopically hairs from the mid-dorsal region of a black-sable mouse which was intermediate in color between black-and-tan and yellow, from pure black-and-tan and from clear yellow mice of the same age. The cause of the difference among the hair colors of these three forms was clearly the varying number of black pigment granules. In the yellow hair the dark granules were extremely rare and poorly defined, appearing in many cases as partially mixed with the diffuse yellow ground color. In the sable hair the black granules were more numerous, occurring singly in the distal third of the shaft, while in the proximal two thirds the concentration was greater. Here the granules were large, one granule usually extending across the medullary space. In some cases two granules appeared side by side, and in rare instances I noted rows of three across the hair. In the hairs from the black-and-tan the concentration of granules was three to ten times as great as in the sable hair; the whole shaft was filled with closely packed small black granules. One row was rare; two was common; the rule was three or four rows, while I sometimes found rows of six small granules packed closely into the width of the hair.

If, as I have stated, there exist in mice genes determining the quantitative increase of dark pigments, it should be possible by experiment to test their existence and to determine whether they are Mendelian in behavior or not and whether they are simple or multiple. The data which follows is submitted as a test of the above questions.

According to the provisional hypothesis, black-and-tan being the darkest member of the series should genetically contain the greatest number of modifying genes. The presence of such genes should become apparent if black-and-tan were crossed with a race containing the dark pigments but lacking entirely any of the modifying genes. These conditions were satisfied only by pure wild house

mice, caught at a distance to insure against any contamination from crossing with fancy varieties. These wild mice were regarded as lacking the darkeners; black-and-tan as containing the maximum concentration of darkeners; and after some preliminary experimentation it was decided that six stages in darkness could be distinguished of which the wild was regarded as grade 1 and black-and-tan as grade 6. These did not represent all the grades that actually appeared, for the variation from one to six was practically continuous but such arbitrary points had to be fixed for convenience in observation and record. These grades were standardized by means of type skins for each grade with which each mouse was compared at the age of three weeks and at later intervals throughout life.

The results of crossing black-and-tan with wild agouti are seen in Table I and Fig. 1. The first generation consisted of two classes of young, darkened yellows and darkened agoutis. The mode of the $F_1$ yellows was at grade 3, and their mean grade was 3.3 both practically midway between the parent grades. The mode of the $F_1$ agoutis was at 2 and their mean grade was 2.8 showing that although they represented a blend between the parental types the agouti pattern affords a less favorable background for the development of darkness than does yellow.

Two $F_2$ generations were raised, one by inbreeding the $F_1$ yellows, the other by inbreeding the $F_1$ agoutis. The distribution of $F_2$ yellows shows the increased variability which we have come to expect from such blending characters as size and other quantitative measurements. Evidence of segregation of parental characters appears from the presence of a large number of grade 1 (yellows) and the separation of this class from the other large class (grades 3 and 4) by a small class (grade 2). Segregation of darkness may also be inferred from the large class at grade 5 which contained relatively few individuals in $F_1$. The mean grade of $F_2$ is 3.0 indicating that the average darkness has not changed while the distribution has changed considerably. The same is true in a lesser de-

gree of the $F_1$ agoutis resulting from the inbred $F_1$ yellows and of the progeny of the inbred $F_1$ agoutis. In the latter class strong evidence of the segregation of the undarkened wild is apparent from the large size of grade 1

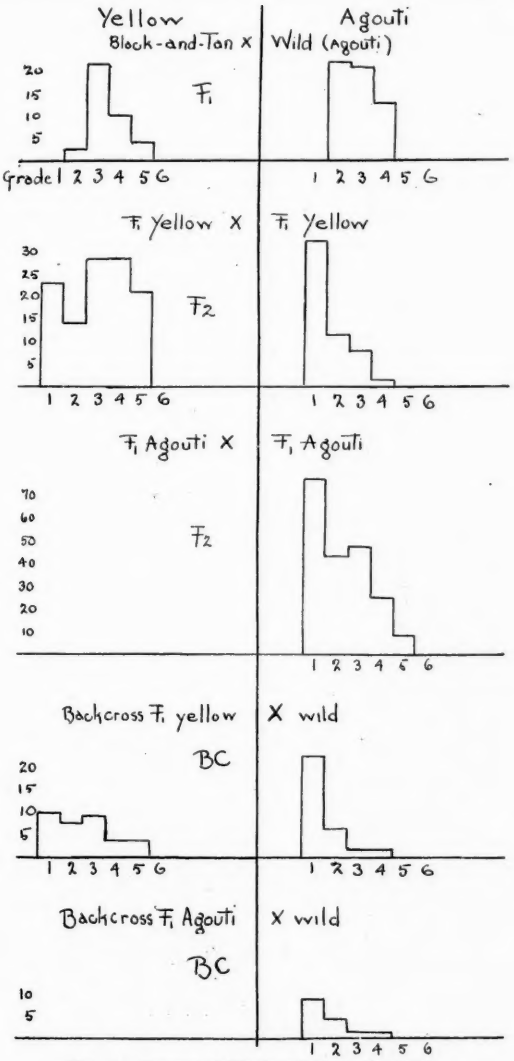


FIG. 1. Crosses of Black-and-Tan with Wild.

## TABLE I

CROSSES OF BLACK-AND-TAN WITH WILD AGOUTI

| Cross Number | Parents by Generation and Grade | Yellow Young by Grades | | | | | | Agouti Young by Grades | | | | | | Total Young | Total Yellow | Total Agouti | Total Black | Mean Yellow | Mean Agouti |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 1 | 2 | 3 | 4 | 5 | 6 | 1 | 2 | 3 | 4 | 5 | 6 | | | | | | |
| | | Yellow | Sooty | Sable | Dk. Sable | Blk-Tan.Lt. | Blk.-Tan | | | | | | | | | | | | |
| I..... | Blk.-Tan (6) × Wild Agouti (1) | | 2 | 21 | 10 | 4 | | | 23 | 22 | 13 | | | 95 | 37 | 58 | | 3.43 | 2.83 |
| II.... | $F_1$ Agouti (2, 3, 4) × Fi Ag. | | | | | | | 78 | 43 | 46 | 25 | 9 | | 211 | | | 57 | | 2.22 |
| III... | $F_1$ Agouti (3) × Wild (1) | | | | | | | 8 | 4 | 1 | 1 | | | 14 | | 14 | | | 1.64 |
| IV ... | $F_1$ Sable (3. 4) × $F_1$ Sable (3, 4) | 23 | 14 | 27 | 27 | 21 | | 33 | 12 | 8 | 1 | | | 166 | 112 | 54 | | 3.08 | 1.58 |
| V .... | $F_1$ Sable (3, 4) × Wild | 10 | 8 | 9 | 4 | 4 | | 23 | 6 | 2 | 2 | | | 68 | 35 | 33 | | 2.54 | 1.49 |
| VI ... | $F_2$ Blk. and Tan (light) (5) × Wild | | | 7 | 1 | | | 4 | | | | | | 8 | 8 | 4 | | 3.12 | 1.00 |
| VII .. | $F_2$ Dk. Sable (4) × Wild | 3 | 3 | 6 | 3 | | | 28 | 2 | | | | | 45 | 15 | 30 | | 2.60 | 1.07 |
| VIII.. | $F_2$ Sable (3) × Wild | 3 | 2 | 2 | | | | 8 | | | | | | 15 | 7 | 8 | | 1.86 | 1.00 |
| IX ... | $F_2$ Sooty (2) × Wild | 4 | 3 | | | | | 8 | | | | | | 15 | 7 | 8 | | 1.43 | 1.00 |
| X .... | $F_2$ Yellow (1) × Wild | 8 | | | | | | 10 | | | | | | 18 | 8 | 10 | | 1.00 | 1.00 |

(wild). The average grade of these $F_2$ agoutis is 2.2, slightly lower than the $F_1$ grade while two new grades have been added to the distribution, grade 1 (wild) and grade 5 (very dark agouti). A few back crosses were made of $F_1$ agoutis with wild, and of $F_1$ yellows with wild. These showed likewise segregation of undarkened yellows and undarkened agoutis and lower mean grades than $F_1$—2.5 for yellows and 1.5 for agoutis.

The results thus far had established the presence of a factor or factors for darkness, the formation of intermediates in $F_1$ when crossed with animals lacking it, and the incomplete segregation of parental types in $F_2$. They had not answered our questions regarding Mendelian behavior or number of factors involved. This failure may have been due to incorrect observation, to the failure of the grading scale to distinguish between the types produced or to the actual non-appearance of the types expected. By constant application and regrading it was believed that the error from the first two reasons was low. To consider the third, one must recall what is known of the origin of the black-and-tan variety. It has been for some years a standard breed of the English fancy, built up probably through the constant selection by breeders of the points it now possesses—clear yellow belly and intensely black back with a sheen not duplicated in any other variety or in the hybrids of black-and-tans with other varieties. Since the variety breeds quite true these points must be heritable, and one can hardly expect to extract the pure type of black-and-tan from a cross with wild without practising upon the segregates a selection similar to that which perfected the variety. This involves the supposition that the factors causing the darkness of the black-and-tan are very numerous and extremely small in individual effect.

The $F_2$ darkened agoutis were chosen as the starting point of a selection for darkness which lasted through several generations. These agoutis were easier to grade because they were non-yellow; their litters were larger for the same reason, and it was also desired to know

whether the fact that black-and-tans were always heterozygous for black was a cause of their darkness. The results of mating together dark agoutis of various grades is shown in Table II and Fig. 2.

TABLE II

CROSSES OF DARK AGOUTIS INTER-SE

| Parents | Grade Distribution of Young | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 5.5 | 6 | Total Ag. | Mean Grade | Blk. |
| XI. 1 × 1 | 32 | | | | | | | 33 | 1.00 | 1 |
| XII. 2 × 2 | 11 | 21 | | | | | | 33 | 1.60 | 1 |
| XIII. 4 × 2 | 11 | 18 | 6 | 3 | | | | 38 | 2.02 | 2 |
| XIV. 4 × 3 | | | 6 | 5 | | | | 11 | 3.45 | 1 |
| XV. 4 × 4 | | | 7 | 6 | | | | 13 | 3.46 | 0 |
| XVI. 5 × 4 | | 1 | 10 | 8 | 16 | 5 | 4 | 51 | 3.83 | 13 |
| XVII. 5 × 5 | | 3 | 17 | 33 | 28 | 18 | 6 | 105 | 4.38 | 18 |
| XVIII. 6 × 4 | | 1 | 5 | 19 | 19 | 8 | 13 | 68 | 4.66 | 2 |
| XIX. 5.5 × 5.5 | | | | 4 | 4 | 8 | 5 | 21 | 5.23 | 7 |
| XX. 6 × 5 | | | 6 | 20 | 41 | 47 | 21 | 135 | 5.09 | 30 |
| XXI. 6 × 6 | | | | 6 | 16 | 23 | 27 | 72 | 5.45 | 18 |
| XXII. 6 × 1 (wild) | 13 | 26 | 19 | 8 | 6 | | | 72 | 2.55 | 0 |
| I. Blk.-tan × wild | | 23 | 22 | 13 | | | | 58 | 2.83 | 0 |

The table shows plainly that the variation in darkness is practically continuous. Animals of grade 1 proved to be pure wild segregates entirely lacking the darkeners. Grades 2, 3 and 4 contained the darkener but never produced by recombination any animals darker than their own grade. Grades 5, 5.5 and 6 produced grades both darker and lighter than their own, proving them to be heterozygous in the modifiers. None of these darkest grades proved to be pure dark segregates. Even grade 6 which was entirely black with a gray belly and quite comparable in darkness to black-and-tan produced animals of grade 1 (light segregates) when crossed with wild agouti. These grade 1 agoutis were tested and found to lack any modifiers for darkness. Therefore grade 6 in darkness was not homozygous as regards the darkening modifiers.

The supposition that the darkness of the dark agoutis might be due simply to their being heterozygous for black was disposed of by the results of the dark agouti crosses, for of eighteen $F_2$ dark agoutis thoroughly tested, twelve were heterozygous for black and six were homozygous

agoutis. In subsequent generations selection was in the direction of darkness. That this was not accompanied by selection of heterozygotes is shown by the figures for dark agoutis of $F_3$, $F_4$ and $F_5$ which were tested. In generations $F_3$ and $F_4$ there were twenty agoutis heterozygous for black to 8 homozygous agoutis; in $F_5$ four heterozygotes to three homozygotes, and the homozygotes com-

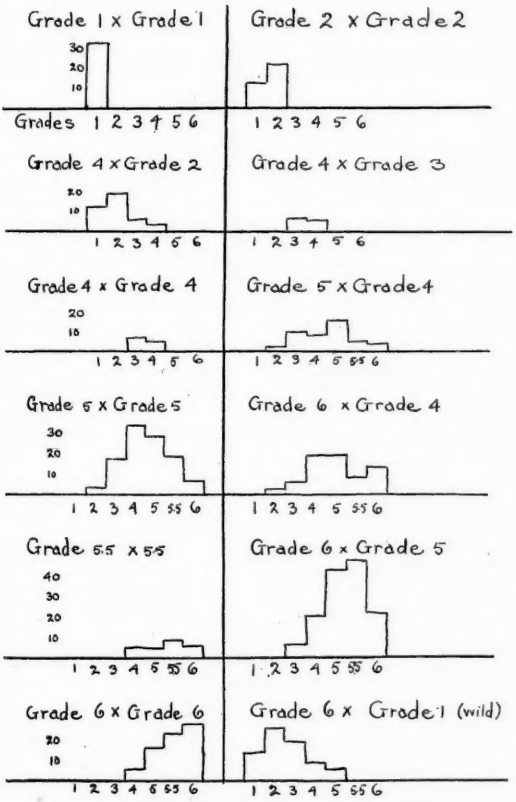
Grade 1 x Grade 1
Grade 2 x Grade 2
Grades 1 2 3 4 5 6
Grade 4 x Grade 2
Grade 4 x Grade 3
Grade 4 x Grade 4
Grade 5 x Grade 4
Grade 5 x Grade 5
Grade 6 x Grade 4
Grade 5.5 x 5.5
Grade 6 x Grade 5
Grade 6 x Grade 6
Grade 6 x Grade 1 (wild)

FIG. 2. Crosses of Dark Agouti Inter-Se.

prised some of the darkest mice produced. Another explanation for the darkness of the agoutis must be invoked and the data indicate that the only alternative is the ac-

quisition by the dark agoutis of the peculiar and puzzling darkness from the black-and-tan race.[1]

Up to his point the data has involved crosses of darkness with its absence—and crosses of dark animals of various grades inter se. Multiple factors appear to be involved and yet no evidence of Mendelian behavior has been adduced except the segregation of lack of darkness without accompanying segregation of darkness.

Many additional crosses have been made in which the darkeners from the sable series have been transferred into other varieties with results similar to those outlined above. The most extensive of these secondary experiments involved crosses of black-and-tan with brown (chocolate) mice to test the black-and-tan (yellow) gamete and to separate if possible the darkening modifiers (see Table III and Fig. 3). This cross brought about the union in the first generation of gametes with full darkness (black-and-tan) with a uniform set of gametes from the brown race all of which supposedly lacked the darkener. The first generation from this cross showed, as was expected, the dominance of black, all young being black pigmented. Approximately one half were self black which on being tested proved to be heterozygous for brown. The other half were a lightened black-and-tan (Table III, cross 23) with some variation but none were as black as pure black-and-tan. The number of dark pigment granules in the dorsal hairs was reduced and the yellow pigment substratum was thereby allowed to show at bases and tips of hairs especially in the older animals. From these light black-and-tans was bred an $F_2$ generation (cross 26) consisting of mice with black pigment and

[1] Morgan in 1914 reported the appearance in his experiments of mice to which he gave the name "new gray," which were noted first in the offspring of a pair of cinnamon mice. They "looked like chocolates, but . . . showed on later inspection distinctly ticked hair. One of these new grays bred to black (heterozygous) gave some chocolates, black, new grays, and one very dark, almost black, mouse." The above descriptions apply quite accurately to cinnamon and agouti mice which I have raised from crosses with one of the sable series and I have little doubt that the darkness of Morgan's new grays was derived originally from some mouse carrying the "darkener."

mice with brown pigment in approximately the ratio 3:1. Of the blacks about one third were self black; the others were yellows, sooties and black sables with varying amounts of black in the fur, much like the $F_2$ array in the

TABLE III

CROSSES OF BLACK-AND-TAN WITH BROWN

| Cross No. | Parents | Yellow and Black Young | | | | | | | | | | Yellow and Brown Young | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 1 | 2 | 3 | 4 | 5 | 5.5 | 6 | Mean | Blk. | Tot. | 1 | 2 | 3 | 4 | 5 | 6 | Mean | Brown | Tot. |
| 23 | Blk.-tan × Br. . . . . | | | | 4 | 17 | 6 | | 4.96 | 19 | 46 | | | | | | | | | |
| 24 | $F_1BT \times F_1BT$. . . . . | 2 | 1 | 2 | 3 | 12 | 26 | 14 | 5.15 | 26 | 86 | 0 | 2 | 1 | 1 | 8 | 10 | 5.05 | 12 | 34 |
| 25 | $F_1BT \times$ brown . . . . | 5 | 3 | 11 | 2 | 4 | 2 | | 3.00 | 30 | 57 | 9 | 2 | 7 | 0 | 10 | | 3.00 | 26 | 54 |
| 26 | BT × Br. and tan 6 | | | | 1 | 1 | 0 | 2 | | 3 | 7 | | | | | | | | | |
| 27 | $F_1BT \times F_1BT$ from cross 26 . . . . . | | | | 1 | 2 | 5 | 17 | 5.74 | 7 | 32 | | | | | 3 | 3 | | 5 | 11 |

black-and-tan × wild agouti cross. In this $F_2$ distribution were seen, besides all grades of intermediates, segregates of both sorts, viz., yellows of grade 1 and black-and-tans of grade 6, although the latter did not retain their darkness throughout life and when bred proved not to be pure segregates. The $F_2$ mice with brown pigment were similarly divided into yellows and brown sables with varying amounts of brown in the fur and self brown in the ratio 2:1. Of the yellow-browns some were evidently counterparts of black-and-tan with the black pigment replaced by brown. To these the name brown-and-tan was given; the other yellow-browns paralleled the yellow-black series although the lower and intermediate grades were less well represented, due perhaps to the difficulty of distinguishing between yellows with considerable brown pigment and yellows with smaller amounts of black pigment. Breeding tests were used in doubtful cases.

The $F_1$ light black-and-tans, when backcrossed to browns (Table III, cross 24), gave equal numbers of all four sorts, viz., yellow-blacks, self blacks, yellow-browns and self browns. The mode of these yellow-blacks was in the middle class (grade 3) in contrast with the mode at 5.5 in the straight $F_2$.

These crosses of black-and-tan with brown show the independence of the darkeners from black pigment for in these experiments the modifiers have been detached from

the black pigment on which they operate in the pure black-and-tan and transferred to brown pigmented yellows where their action is similar. Their independence of yellow was illustrated by their action on agouti mice.

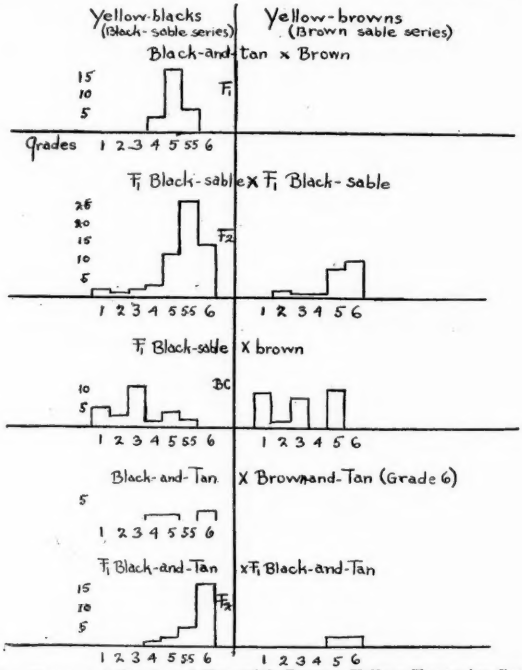
Yellow-blacks (Black-sable series)
Yellow-browns (Brown sable series)
Black-and-tan × Brown
F1
Grades 1 2 3 4 5 55 6
F1 Black-sable × F1 Black-sable
F2
1 2 3 4 55 6
1 2 3 4 5 6
F1 Black-sable × brown
BC
1 2 3 4 55 6
1 2 3 4 5 6
Black-and-Tan × Brown-and-Tan (Grade 6)
1 2 3 4 55 6
F1 Black-and-Tan × F1 Black-and-Tan
F2
1 2 3 4 55 6
1 2 3 4 5 6

FIG. 3. Crosses of Black-and-Tan with Brown, Yellow Young by Grades.

The intermediate nature of $F_1$ in the black-and-tan × brown cross and subsequent segregation of dark and undarkened forms is not as clear as in the agouti crosses, for it is probable that the brown parent contributed factors comparable to the darkeners which have acted to make both $F_1$ and $F_2$ darker than if the darkening factors had come only from the black-and-tan parent. The browns used were derived from a yellow variety known as red. Both the reds and their brown recessives are more intensely colored than any other yellows or browns, and in fact have given evidence in later experiments of differing from ordinary varieties by intensity factors similar to the darkening factors of black-and-tan.

The results throughout indicate that we are dealing here with genetic factors similar to those which have produced such quantitative differences as size in the races of rabbits studied by Punnett. The results obtained from crossing large and small races of rabbits agree in the production in $F_1$ of animals genetically intermediate between the parent races, and in the evidence of subsequent segregation of the smaller size without segregation of the larger. The same phenomenon appears in the present study for light segregates have appeared but never the dark. Placing the causes of darkness in mice in the same category with the causes of size differences, which have not yet been made clear, is an admission of the unsuitableness of the material rather than of the insoluble nature of the problem. Either the best material for the investigation of such grade variations has not yet been found or else the technique of observation and measurement of such genetic differences as distinguished from non-heritable differences has not yet been evolved. The correct interpretation of such differences must await an investigation combining an optimum of material and method.

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# SHORTER ARTICLES AND DISCUSSION

## HYBRIDIZATION AND EVOLUTION

SOME years ago the writer made a cross between the two species *Nicotiana rustica* L. and *Nicotiana paniculata* L.[1] Since the hybrids obtained through this mating are not completely sterile, some biologists may perhaps maintain they are not distinct species, but such a claim is wholly arbitrary. In a sense, a species is a human concept and as such its definition may be carried to any ridiculous extreme, yet there is no more striking biological fact than that *in general* the great groups of living things do fall into specific subdivisions which many criteria show to be distinct, discontinuous, without intermediates. In two such groups fall the above types. Though their ranges overlap, they differ from each other in leaf, stem, flower and habit of growth much more than do several other pairs of species within the same genus between which hybridization is impossible, or where the hybrid is sterile.

The cross between these two species gives an $F_1$ generation intermediate between the two parents, and as uniform in each character as either parental group.

Few of the male or the female gametes are viable, yet by careful attention to pollination, from one to twenty seeds can be obtained in the capsules, where normally two hundred to three hundred seeds are found. These seeds produce an $F_2$ generation which is inordinately variable. No two plants are similar, and numerous types can be picked out which if found in the wild would undoubtedly be classed as different species. In genetic terms, the behavior of the two species may be described as follows: They differ in an extremely large number of inherited factors; and owing to these numerous differences, many of the otherwise possible combinations of $F_1$ gametes, are not functional. A huge percentage of expected combinations of both gametes and zygotes are thus eliminated.

The factors which in combination produce normal fertility,

[1] A detailed account of the genetic facts found in this study, has not yet appeared. A preliminary paper was published in the *Proc. Amer. Phil. Soc.*, 54: 70–72, 1915.

recombine in the Mendelian sense, quite as do the factors controlling the form of leaf and flower. The result is that after a few generations of selection one may obtain a variety of strains, uniform within each line, so fertile as to yield capsules with over ninety per cent. of the normal quota of seed, and so different from one another that the extreme types are more unlike than the two original species used in the cross.

After three years of selection ($F_5$), eight such strains remained out of a large series of selections studied earlier. It seems hardly necessary to describe the differences they exhibited. Suffice it to say that the smallest type was about 20 cm. in height with small smooth oval leaves, and the largest was nearly 200 cm. in height with wrinkled cordate leaves some of which were 50 cm. in length.

*These eight strains were crossed in all possible combinations, and every $F_1$ generation exhibited as high a degree of fertility as that shown by the parents.*

To the writer it seems possible that these results have a bearing on certain theoretical problems which may not be clear at first sight.

A few years ago Lotsy[2] published an extended paper based on a very limited number of crosses in the genera *Nicotiana, Pisum, Petunia* and *Antirrhinum,* where partially sterile $F_1$ plants produced exceedingly variable progeny,—results wholly comparable with our own. From these observations, neglecting all evidence of the appearance of mutations in controlled pure lines, Lotsy founded a theory of evolution. His arguments were based upon five assumptions: (1) that all characters obey the Mendelian law of heredity, (2) that acquired characters are never transmitted, (3) that homozygotes are absolutely constant in succeeding generations, (4) that there has been no proof of variation independent of crossing, and (5) that the variations observed after crossing are sufficient to account for evolution.

Naturally numerous criticisms can be made against this extreme interpretation. One need only inquire as to the source of the original variations which are to form the basis of all Mendelian recombinations, to show the untenability of the position. On the other hand, it will be admitted by all that hybridization has played some part in evolution, and it is of some importance to endeavor to determine the limits of its rôle.

[2] Lotsy, J. P., "La théorie du croisement," *Arch. Néerland. Sci. Exact. et Nat.,* III, B, 2: 1–61, 1914.

The observations of the writer on the enormous variability of the $F_2$ generations arising from partially sterile $F_1$ generations produced by crossing species, led him to suspect that such combinations might be the basis of a great deal of variability responsible for evolution under domestication. A careful survey of the evidence relating to the origin of modern horses, cattle, sheep, swine, dogs, guinea pigs, fowls, ducks, and geese on the one hand, and varieties of wheat, corn, barley, oats, rye, apples, grapes, roses and begonias on the other hand, shows that in every case several related wild or semi-wild species exist which will cross together and yield partially fertile offspring. Doubtless many other species which have shown great improvement under domestication, would be found to have wild relatives which behave similarly, should they be investigated. Both the historical and the experimental evidence, therefore, point to hybridization, and particularly to species of hybridization, as the great single cause of evolution under domestication.

At the same time, one must not confuse evolution under domestication with natural evolution. The outstanding biological feature characteristic of the varied groups of domestic animals and of cultivated plants, is the perfect fertility within each group. A marked peculiarity of the great majority of natural species is their sterility with one another, the origin of which has long been a stumbling block to writers on evolutionary biology. Our own experimental evidence, as far as it goes, and observations on domestic forms which presumably have originated from combinations of two or more wild species, yield not the slightest indication of a tendency toward the production of segregates that exhibit either incompatibility in crosses or sterility of the individuals produced by hybridization.

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## THE MEASUREMENT OF LINKAGE

LINKAGE is a name for that tendency sometimes shown by genes to maintain in hereditary transmission their previous relations to each other. Thus if two linked genes, A and B, enter a cross together, in the same gamete, they will oftener than not be found together in the gametes formed by the cross-bred individual. And if the same two genes enter the cross separately,

one in the egg, the other in the sperm, then oftener than not they will be found apart, in different gametes formed by the cross-bred individual.

Where no linkage exists between two genes, A and B, it will be wholly a matter of chance whether they go together or not, no matter what their previous relation was. We say that they "assort independently," as genes do in ordinary Mendelian inheritance, such as was known to Mendel. In such cases change of relation occurs in the long run in half (or 50 per cent.) of all cases. Such change of relation is called "crossing over." Linkage evidently will be shown by a falling below 50 in the percentage of cross-overs. The more cross-overs decline below 50 per cent., the stronger will be the linkage indicated, until when no cross-overs occur, we call the linkage complete or perfect. Accordingly 0 and 50 per cent. will be the limiting values for cross-overs indicating linkage. But it is conceivable that cross-overs might occur in excess of 50 per cent. What would their significance be? Not linkage, not a tendency to maintain relations previously existing between genes, but a tendency to *change* those relations, to go apart when previously together, and to get together when previously apart. We are not acquainted with any such tendencies as these, and it is difficult to imagine how they might arise, but it is certain that they would be the opposite of linkage and would need a different name, if observed.

It is evident that the strength of linkage increases, as the cross-over percentage decreases below 50. As a measure of the strength of linkage, we might then take the difference between 50 and the observed cross-over percentage, as I have elsewhere suggested (Castle, 1919). This would give us a numerical grade of linkage strength on a scale of 50. But since we are more accustomed to grading on a scale of 100, it will perhaps be better to double values thus obtained. Our grading scale of linkage strengths will then run thus:

| Cross-over Percentage | Linkage Strength |
|---|---|
| 50 | 0 |
| 40 | 20 |
| 30 | 40 |
| 20 | 60 |
| 10 | 80 |
| 0 | 100 |

By this method we can compare the linkage strength between

any two pairs of genes without stopping to reverse the relations indicated by cross-over percentages. For example the following linkage relations are shown by the genes of rats and mice (Dunn).

| Genes | Cross-over Percentage | Linkage Strength |
|---|---|---|
| Albinism—red-eye, rats | 1.8(?) | 96.4 |
| Red-eye—pink-eye, rats | 18.3 | 63.4 |
| Albinism—pink-eye, rats | 21.1(?) | 57.8 |
| Albinism—pink-eye, mice | 14.6 | 70.8 |

The strongest linkage here indicated is that between albinism and red-eye in rats, next comes that between albinism and pink-eye in mice. But albinism and pink-eye in rats show less linkage than in mice. The three genes, albinism (*c*), red-eye (*r*) and pink-eye (*p*) in rats are apparently arranged in linear fashion thus:

```
c.....r.....p
0     2(?)    21
```

This kind of a diagram is what Morgan, Bridges and Sturtevant (1919) have made familiar to us under the name of "chromosome map." Not to prejudice the case for or against the chromosomes, we might perhaps call it a linkage map or map of a linkage system. In its construction we use cross-over percentages as direct measures of map distances, but in *Drosophila* at least only distances relatively short have been found to be strictly comparable. Beyond distances of about 5 units (cross-over percentages) it is found that double or triple cross-overs become increasingly common and thus decrease the apparent number of breaks in the linkage chain between two genes. So that long map distances are based, not on directly observed cross-over percentages between the more distant genes, but on summation of intervening short distances, it being assumed that the arrangement is in all cases linear. While this latter assumption is not to be accepted for all cases without proof, it must be admitted that for *Drosophila* at least the evidence for a linear arrangement is very strong and no insuperable objections can be raised against it.

Map-distances have been found in the "first chromosome" linkage group of *Drosophila* exceeding 60, and in the "second chromosome" group exceeding 100. But in no case does the observed cross-over percentage between two genes, however remote, of the same linkage group exceed 50. This means that

beyond very short distances cross-over percentages do not increase in proportion to distance. The linkage group forms a means of holding genes together, however distant they may be from each other, so that, as one goes, all have a tendency to go. The linkage map will give us a diagrammatic view of the relations to each other of the genes composing a linkage system. It is based on the *shorter observed cross-over percentages*, or where longer distances are used, they must be first corrected for double and triple crossing-over. See in this connection the valuable Table II. of Haldane (1919) which provides a ready means of converting map distances into cross-over percentages or *vice versa*, and so of predicting undetermined linkage relations. It is based on a mathematical examination of the linkage system of the first chromosome of *Drosophila*. A table of linkage strengths will show us, without reference to distances involved, to what extent the movements in gametogenesis of one gene are correlated with those of any other gene. It is based on the *unmodified cross-over percentages observed*, whether the map distances involved are great or small. Linkage strengths can never exceed 50 on a scale of 50, 100 on a scale of 100, whereas map-distances may be extended indefinitely with the discovery of new genes.

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## IS THERE LINKAGE BETWEEN THE GENES FOR YELLOW AND FOR BLACK IN MICE?

IN a recent number of this journal Dunn[1] has given data showing a deficiency of black young in a family of yellow mice.

[1] AM. NAT., 53: 558–560, 1919.

Thus in a cross of two yellows, one of them probably heterozygous for both black and brown and the other for brown only, the offspring totalled fourteen yellow and four brown, the expectation being twelve yellow, three black and three brown. The yellow descendents of this mating when bred to browns are expected to give two yellows (one heterozygous for both black and brown and one heterozygous for brown only) to one black to one brown. The actual numbers obtained were eighteen yellow, one black, and ten brown, and the expected numbers fourteen yellow, seven black and seven brown. Dunn has summarized these data according to the percentage of young of each sort produced, as follows:

| | Yellow | Black | Brown |
|---|---|---|---|
| Per cent. expected | 66.6 | 16.6 | 16.6 |
| Per cent. observed | 62.0 | 3.4 | 34.5 |

In the total number of young observed, the chances are equal that the 16.6 per cent. expected black young might go as high as 30.8 per cent. or as low as 2.4 per cent. It is therefore apparent that neither the 3.4 per cent. black nor the 34.5 per cent. brown are significantly outside the limit of probable variation due to chance.

Although not including chance fluctuation as one of the three theories capable of explaining his observed facts, Dunn evidently feels the need for larger numbers of young before considering random sampling eliminated.

It is interesting however to see just what evidence there is in Dunn's data that black and yellow are linked. Apparently the only facts in support of this hypothesis is the deficiency of blacks and the slight excess of browns referred to. Significant evidence for the expected excess of yellows carrying both black and brown as compared with those carrying brown only is not obtained. Of seventeen such yellows tested, ten carried both black and brown and seven brown only—exact equality or 8.5 of each is the Mendelian expectancy. The excess of yellows carrying black and brown is 8.8 per cent. as against non-yellow browns of 17.9 per cent. The deficiency of yellow carrying brown only is 8.8 per cent. as against a deficiency of blacks of 13.3 per cent. The sum of the departures from the expected equality in *yellows* is 17.6 per cent., while in *non-yellows* it is 31.2 per cent., or almost twice as much. The discrepancies in the yellow indi-

viduals are even more within the possibility of chance fluctuation than those of the non-yellows.

Dunn states that linkage between Y and B "affords a satisfactory explanation of the observed facts in harmony with other cases of linkage." However, one of the essential points of linkage is that members of a multiple allelomorph series are linked to a given gene in the same degree. Cuénot,[2] Morgan,[3] Sturtevant,[4] and the writer,[5] have shown that the genes for yellow and for agouti in mice are allelomorphic. Many investigators, including Durham,[6] Detlefsen,[7] and the writer,[8, 9] have shown that agouti and black are not linked in inheritance—yet according to our present knowledge of linkage all genes in the same locus are equally linked with any other given gene, and these crosses should show linkage between agouti and black to a degree equal to that of linkage between black and yellow. Dunn has not emphasized this point sufficiently.

Furthermore, if there is any significance other than random sampling in the peculiar ratios reported, there is another possible explanation, not considered by Dunn, which avoids hypothecating linkage between yellow and black. If a lethal factor was closely linked with black in the particular family under consideration, and if this lethal was effective in a heterozygous condition in non-yellow mice—but not in yellow mice, the observed results would be explicable as follows:

| | |
|---|---|
| Let Y equal yellow, | y equal non-yellow. |
| B equal black, | b equal brown. |
| L equal lethal, | l equal normal. |

Yy $\widehat{BL}$ $\widehat{bl}$ equals yellow heterozygous for black and lethal.
Forms gametes:

| | | | |
|---|---|---|---|
| $Y\widehat{BL}$ | commonly | $Y\widehat{bL}$ | rarely |
| $y\widehat{BL}$ | | $y\widehat{bL}$ | |
| $Y\widehat{bl}$ | | $Y\widehat{Bl}$ | |
| $y\widehat{bl}$ | | $y\widehat{Bl}$ | |

[2] *Archiv Zool. Exp. et Gen.* (4), Vol. 8, 1911.
[3] AM. NAT., 48, pp. 449–458, 1914.
[4] AM. NAT., 46, pp. 368–371, 1912.
[5] *Sci.*, N. S., 38, p. 205, 1913.
[6] *Jour. Genet.*, I, pp. 159–178, 1911.
[7] *Genetics*, 3, pp. 573–598, 1918.
[8] Carn. Inst. of Wash., No. 179, 1913.
[9] AM. NAT., 47, pp. 760–762, 1913.

Crossed with brown normal yy$\breve{b}\breve{l}b\breve{l}$ such a yellow would give the following zygotes:

| | | |
|---|---|---|
| Yy $\hat{B}\hat{L}$ $\hat{b}\hat{l}$ | Yellow heterozygous for black and lethal | *commonly.* |
| yy $\hat{B}\hat{L}$ $\hat{b}\hat{l}$ | *Black lethal; dies** | |
| Yy $\hat{b}\hat{l}$ $\hat{b}\hat{l}$ | Yellow carrying brown normal | |
| yy $\hat{b}\hat{l}$ $\hat{b}\hat{l}$ | Brown normal | |
| Yy $\hat{b}\hat{L}$ $\hat{b}\hat{l}$ | Yellow carrying brown and lethal | *rarely.* |
| yy $\hat{b}\hat{L}$ $\hat{b}\hat{l}$ | Brown lethal; dies* | |
| Yy $\hat{B}\hat{l}$ $\hat{b}\hat{l}$ | Yellow normal heterozygous for black | |
| yy $\hat{B}\hat{l}$ $\hat{b}\hat{l}$ | Black normal | |

The death of the rare brown lethal individual would not be noticed, for the common death of black lethals would leave a distinct excess of brown normals.

This hypothesis is capable of experimental test and involves a lethal mutation in an entirely new factor which presupposes no generality of the process in all yellows and agoutis; and simply assumes that yellow, when present, hampers the action of the lethal in much the same sort of way that it hampers the activity of the black forming factor in the skin and hair.

The above hypothesis is advanced simply as an additional possibility for test in case something more than chance fluctuation due to random sampling is involved.

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## CREPIS—A PROMISING GENUS FOR GENETIC INVESTIGATIONS

To all who are familiar with the recent advances in our knowledge of heredity, which were made possible largely through the investigations of Morgan and others with the fly, *Drosophila melanogaster,* especially to those who have followed the development of the chromosome theory of heredity with its correlative theories of mutation and evolution, the urgent need of extensive corroborative evidence from other animals and plants must be forcibly clear. Although it appears inconceivable that the conclusions reached from the drosophila investigations are not applicable in all their essential features to all animals and plants,

yet it can not be denied that many biologists are not yet committed to the acceptance of these conclusions as of general application. It is obvious that extensive corroborative evidence, derived from other genera of animals and plants, would be of paramount value in firmly establishing these far-reaching conclusions. It, therefore, becomes one, who allies himself with those biologists who believe in the present importance and future promise of this collection of genetic evidence, derived as it is, almost entirely from a single species of insects, to consider most carefully the selection of other material with which to test the various hypotheses that have been proposed in order to interpret the great mass of drosophila data consistently.

It is encouraging to note the energetic efforts of a number of investigators to obtain a corresponding collection of data from other species of *Drosophila.* As yet, however, little more than a beginning has been made, particularly with the genetic investigations on these species, because it is necessary first to find the comparatively rare mutant individuals with which to experiment. No other genus of animals thus far reported upon possesses so many features favorable to genetic study as does *Drosophila,* although it is probable that other of the lower animal groups will in time furnish material just as valuable. In plants, the only species in which genetic analysis has proceeded far enough to establish the identity of a considerable number of hereditary factors or genes, are the garden pea, sweet pea, snapdragon, maize, barley and wheat. In most of these and in some other plants evidence of linkage of characters in inheritance has been obtained, but in none has the number of linked groups been shown to correspond with the number of chromosomes in the germ cell and because of the relatively large number of chromosomes in these species it will probably be some time before any considerable body of corroborative evidence can be accumulated from them.

In addition to a low chromosome number there are several other desiderata which the ideal form for genetic investigations should possess. It must display numerous germinal variations. It must be prolific and easily reared. It should have a short life cycle so as to permit of the maximum number of generations within a given time. Furthermore, in the case of a plant, it should be self-fertile, so as to permit of establishing pure lines; it should be easily hybridized; and it should flourish when grown under glass.

A brief life cycle is extremely important because numerous generations must be raised in order to secure adequate data for the analysis of more complicated genetic problems. In this respect, no sexually propagated flowering plants can compare with the insects. On the other hand, certain highly desirable features possessed by plants are either impossible or very difficult of realization in animals. For example, asexual reproduction can often be resorted to in plants when it is desired to perpetuate a particular individual for comparison with later generations. But the most important point of superiority of plants over insects for genetic study is the greater possibility in plants of securing hybrids between different species. That this advantage should receive considerable weight will be admitted by all who recognize the need of studying hybrids between species having different chromosome numbers. The desirability of such investigations has been mentioned recently by Morgan (1919) as follows:

> The theory that the chromosomes are made up of independent self-perpetuating elements or genes that compose the entire hereditary complex of the race, and the implication contained in the theory that similar species have an immense number of genes in common, makes the numerical relation of the chromosomes in such species of unusual interest. This subject is one that could best be studied by intercrossing similar species with different numbers of chromosomes, but since *this would yield significant results only in groups where the contents of the chromosomes involved were sufficiently known to follow their histories,* and since as yet no such hybridizations have been made, we can only fall back on the suggestive results that cytologists have already obtained along these lines.

I have italicized one clause in the above paragraph in order to emphasize the importance of extensive genetic analysis in those particular species which are to be used in intercrossing experiments. It is not sufficient that the species have low numbers and different numbers; it is also necessary that the inheritance of a sufficient number of characters in each species be studied so as to establish the linked groups of characters or genes corresponding to the chromosomes of each species. Only then can the contents of the chromosomes involved be sufficiently known to follow their histories in the hybrids.

Thus we find several excellent reasons for seeking among plant materials for a group of species which possess as many as pos-

sible of those features most favorable to securing the desired results.

With this explanatory introduction let us consider briefly the present state of our knowledge of *Crepis* with reference especially to its promise of usefulness in genetic studies.[1] This genus belonging to the chicory tribe of the Compositæ contains about 200 species (according to Index Kewensis) which are widely scattered, the genus being represented by indigenous species in every continent and in Australasia. Just how great is the diversity in morphological characters within the genus remains to be seen, but the wide distribution of the group as a whole and of some of the individual species would lead one to expect a large number of diverse characters and many different combinations of the same. The descriptive connotation of many of the specific names also indicates a remarkable diversity among these forms. For example, there are giants and pigmies, there are forms with bristly, woolly, floury, and glandular pubescence as well as glabrous forms, there are four or more flower colors and one species is named "bicolor." This expectation has been borne out by such observations on preserved and living specimens as the writer has been able to make. There are annual, biennial and perennial species which should prove to be very interesting forms for interspecific hybridization studies. Finally, within at least two of the individual species, there certainly exists a remarkable diversity of forms.

But it is not for its wealth of variation alone that this genus is especially interesting to geneticists. The cytological investigations which have been made on a dozen or more species of *Crepis* reveal a most interesting situation as regards chromosome numbers. There is at least one species (possibly two or three) having only 3 for the haploid number of chromosomes, a group of six or seven species with 4 chromosomes, another group of four species with 5, a single species with 8, another with 9, and still another with 20 chromosomes as the reduced number. The absence of a common denominator greater than one for this series of numbers has caused some interesting speculations as to the method of derivation of one species from another (Rosenberg, 1918). Several cytologists have also noted the fact that the chro-

[1] This paper is a preliminary communication offered mainly for the purpose of calling attention to this promising material. A few species have been under investigation at the University of California for about three years and will be discussed more fully in a future publication.

mosomes themselves in these species are unusually favorable objects of study, one of my correspondents going so far as to predict that in time *Crepis* will become as famous and useful for laboratory work as *Ascaris* is to-day. But the important consideration in the present discussion is the fact that we have here several species with the same chromosome number as *Drosophila melanogaster* and at least one species with one less chromosome pair. Obviously, if some of these species with the smallest chromosome numbers are highly variable, existing in a large number of distinct varieties or forms, they should serve as excellent material for genetic study especially if they possess the other advantageous features already mentioned.

For at least two such species I can report very great promise as objects of genetic research. *Crepis capillaris* (*virens*)[2] with three chromosome pairs (Rosenberg, 1909, 1918; Digby, 1914) and *C. tectorum*[3] with four pairs (Juel, 1905; Rosenberg, 1909, 1918) both exhibit polymorphism to a remarkable degree. This is evidenced by the diversity of forms referred to these species in the herbaria of the Royal Botanic Gardens at Kew and of the Museum of Natural History in Paris. In both species it seems to be merely a matter of sufficiently extensive seed collection that is required in order to secure a sufficient number of allelomorphic pairs of characters to make possible the desired genetic analysis. My cultures of *C. virens*, which have been grown from seed secured from various foreign countries as well as in California, have already yielded several pairs of contrasted characters which will soon furnish a nucleus of genetic data on this species.

These two species are also very prolific, considering the plant as a whole, there being several or many heads on a plant and each head bearing 5 to 15 fertile achenes in *virens* and 30 to 40 in *tectorum*. Unfortunately an individual flower produces but a single seed and the flowers are so small as to make the work of hybridization rather tedious when absolute control is exercised through castration of the unopened flower. But, while this method is essential in original crosses, it usually is not necessary to castrate many flowers for any one cross, and when it comes to

[2] The nomenclature of this species is somewhat in doubt. Both Robinson and Fernald (1908) and Britton and Brown (1918) name it *C. capillaris* (L.) Wallr., but certain European botanists seem to have retained the name *C. virens* L. for this species.

[3] *C. tectorum* L.

making back crosses on a large scale, it may be practicable to depollinate the flowers of the intended female parent with a water jet instead of actually castrating the buds.

As regards other desiderata to be considered in selecting material for genetic study these two species are very promising. They are easily reared in greenhouse or field, the seeds germinating quickly in glass germinators, thus permitting easy manipulation and careful checking of viability when desired. The life cycle varies from three to six months except in rare cases of retarded development and little or no rest period is necessary in the seed stage, so that it is possible to grow two or three generations in a year with proper facilities for culture under glass. Partial or complete self-fertility is the rule in both these species, although in some strains of *virens* the individual plant is nearly self-sterile. No evidence of parthenogenesis or apogamy has been found in these species. In general, therefore, it will be possible to secure numerous sexually propagated pure lines, differing from one another in one or more allelomorphic pairs, which will serve as the basic material for working out the "chromosome content" in these species. It is only the problem of securing seed from a large number of different localities and of growing and carefully studying a sufficient number of plants that must be solved in order to furnish the pure lines desired. The sooner this can be accomplished the sooner can the extensive analysis of the chromosome content of these species be gotten under way. Finally the critical question as to whether these two species can be hybridized has been answered in the affirmative by the preliminary experiments of the present year.[4]

Sufficient has been said, I trust, to convince the reader that we have in *Crepis* a wealth of material which may fairly be expected to furnish data of the greatest value in testing the generality of the chromosome theory of heredity, and that this group is unique in the promise it holds of carrying out that test in much shorter time than would be required if we should depend only on the data which is slowly accumulating from other plants now under investigation. It should be clearly realized, however, that to accomplish the results aimed at, even with *Crepis*, will require a considerable period of time, the length of the period being largely conditioned by the number of investigators attacking the

[4] Since the above was written difficulty has been encountered in inducing these hybrid seedlings to develop beyond the cotyledon stage. If this difficulty can not be overcome both species will be crossed with still other species having low chromosome numbers.

problem and the facilities at their disposal or, in other words, upon the amount of funds available for this project.

In order to advance the genetic analysis of *Crepis virens* and *C. tectorum* now under way to a stage favorable to carrying out the interspecific hybridization studies properly, calls for greenhouse equipment, technical assistance, supplies and labor which are not at present available. Some provision for the collection of seed in foreign countries should also be made. There is no prospect at this time that these facilities will become available in the near future. It is recognized that the expansion of this project will require a larger proportion of the time of the two investigators now engaged on it and the workers concerned stand ready to meet this requirement.

My purpose in going thus into detail is two-fold. First, so far as I am aware, no other geneticists are working extensively with this genus, and it should be clearly understood that under existing circumstances there is little prospect of rapid progress with my own investigations. Yet the work has gone far enough to accumulate material of very great promise. It is hoped, therefore, that means will be found to support adequately the investigations of *Crepis virens* and *C. tectorum* now under way. Second, it is highly desirable that other geneticists also contribute to the analysis of the two species named above and especially that they proceed with similar investigations, accompanied of course with cytological studies, on other species of *Crepis*.

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## THE INHERITANCE OF CONGENITAL CATARACT IN CATTLE[1]

CATARACT in mammals may be due to environmental causes, or it may be hereditary. The mode of inheritance has been debated. In the case of man Bateson (1) and Davenport (2) regarded cataract as a dominant Mendelian character, while Jones and Mason (3) in an analysis of human pedigrees collected by Harmon (4) concluded that cataract is probably a simple recessive. Danforth (5) raised some pertinent objections to this latter hypothesis, and Jones and Mason (6) later admitted the validity of some of these objections. There are a number of elements in this analysis of human pedigrees which are no doubt perplexing, but the preponderance of evidence seems to favor the hypothesis that cataract in man is a Mendelian recessive.[2] Hereditary cat-

[1] Paper No. 10 from the Laboratory of Genetics, Illinois Agricultural Experiment Station.

[2] The data as analyzed by Jones and Mason seem convincing because of the large value of $P$, a measure of goodness of fit of the observed to the calculated series. While there can be little doubt but that the observed results lie within reasonable limits of error when tested by any one of several approved methods, it should, perhaps, be stated that Jones and Mason's use of Pearson's criterion is hardly justified, inasmuch as Pearson's formula applies to a correlated system of variables in which the sum of the observed frequencies = sum of calculated frequencies, and the sum of the errors = 0. Harris (7) pointed out the value of Pearson's formula in relation to Mendelian ratios. Now in any complex Mendelian ratio of the form $(\frac{1}{2}+\frac{1}{2})^n$ or $(\frac{3}{4}+\frac{1}{4})^n$ where $n$ = the number of allelomorphic pairs and where all terms of the ratio are given, the above conditions are always met. However, the observed series which Jones and Mason attempted to fit to a calculated series is neither a complete Mendelian ratio nor does it fulfill the conditions stated. Jones and Mason were not satisfied with the goodness-of-fit value when the heterozygotes were mated *inter se* ($P = 0.418$), but if the deviations were due to random sampling we should expect the values of $P$ to fluctuate around 0.5. Their results would therefore be interpreted as consistent with their theory, if their method were correct. By using the method adopted by Jones and Mason, one might nevertheless obtain a better (?) fit in this case and thus a more satisfactory result if one dealt with the series of normals in this population rather than the series of cataractous. In any monohybrid ratio, the deviation of the dominant class is equal to the deviation of the recessive class. Hence, if we divide the same series of deviations all the way through by a series of larger calculated values for normals, then $X^2$ will be perceptibly smaller and P larger ($P = 0.71$ in this case). This procedure would be somewhat comparable to stating that in a single toss of 8 coins, 5 heads are more likely to appear than 3 tails, or in a single throw of n coins (n–p) heads are more probable than p tails.

aract is known in some mammals other than man, but little is known regarding its transmission. Hurst (8) stated that liability to cataract-blindness in horses is a Mendelian character.

The data forming the basis of this paper arose through the circumstance that a registered Holstein-Friesan bull, E. T. H. (Holstein-Friesan Herdbook No. 62924) transmitted desirable economic dairy characters to a marked degree, and consequently attempts were made to fix his characters by inbreeding. A number of cataractous offspring resulted from these close matings. The simultaneous occurrence of several cataracts in the progeny of a single bull could not be attributed to chance environmental or intrauterine conditions; hence the pedigrees of all animals involved were carefully studied. There was no record of cataract in any of the ascendants. The original bull, E. T. H., had been mated to a large number of unrelated cows and produced 93 normal $F_1$ offspring. Thirty-two of these $F_1$ daughters were mated to an $F_1$ son and produced 63 $F_2$ calves, of which 55 were normal and 8 showed well-defined congenital cataracts of the stellate type.[3] The ophthalmological aspects of these cases have already been described by Small (8).

Cataract is evidently *recessive* in cattle and if it is a simple Mendelian recessive then the original progenitor, E. T. H., was heterozygous, Nn, where N = normal and n = cataractous. Mated to unrelated normal females, NN, we should expect the 93 $F_1$ offspring to be perfectly normal, but of two genetic types in equal numbers, NN + Nn. In selecting any $F_1$ son to breed to the $F_1$ daughters, it was equally probable that he would be either a homozygous normal, NN, or a heterozygous normal, Nn. A single $F_1$ son, also a registered Holstein-Friesan bull, V. H. (Holstein-Friesan Herdbook No. 158293), was chosen and he proved to be heterozygous. Since half of the $F_1$ daughters were homozygous and half were heterozygous, the former would produce gametes, N + N, and the latter would produce gametes, N + n. The total population of $F_1$ daughters would therefore produce three times as many normal as cataractous gametes. In Mendelian notation the $F_1$ matings were as follows:

$$\tfrac{3}{4}N + \tfrac{1}{4}n = \text{gametes from } F_1 \text{ females},$$

[3] The writers are indebted to Dr. C. P. Small, of Chicago, Illinois, for identifying the type of cataract and for much additional information, and wish to express their appreciation of the deep interest Dr. Small has shown in this case.

$$\tfrac{1}{2}N + \tfrac{1}{2}n = \text{gametes from } F_1 \text{ males,}$$

$$\underbrace{\tfrac{3}{8}NN + \tfrac{4}{8}Nn}_{\text{normal}} + \underbrace{\tfrac{1}{8}nn}_{\text{cataractous}} = F_2 \text{ zygotes.}$$

That is, 7/8 of the $F_2$ calves should be normal and 1/8 should be cataractous. The observed results agree with the calculated rather better than one would usually expect, for the observed = 55 normal + 8 cataractous and the calculated = 55.125 normal + 7.875 cataractous. The 8 $F_2$ cataractous calves were of both sexes (2 heifers and 6 bulls).

All these facts clearly indicate that the original sire, E. T. H., was heterozygous, Nn. If mated to his own daughters he should give results similar to those of his son, V. H. He was thus tested and produced 7 offspring of which 3 (1 bull and 2 heifers) were cataractous. Collecting all matings of the sire, E. T. H., and his son, V. H. (both were Nn) to $F_1$ daughters (NN + Nn) we found:

| | Normal | Cataractous | Total |
|---|---|---|---|
| Observed | 59 | 11 | 70 |
| Calculated | 61.25 | 8.75 | 70 |

We may therefore conclude that congenital cataract in cattle is a simple recessive Mendelian character.

To prevent the reappearance of cataractous individuals in this stock and to reduce the proportion carrying cataract as a recessive is a matter of some economic importance. After all cataractous individuals have been eliminated, there still remain one half of the daughters and four sevenths of the granddaughters of E .T. H. which carry a recessive factor for cataract. We can not distinguish between the NN and Nn individuals, since N is evidently dominant to n. Whatever the proportion of these two types may be to each other, mating the cows to normal unrelated bulls (which are almost unquestionably NN) will eventually reduce the cataractous-bearing individuals to a negligible minimum. If we begin with r + s individuals of the genetic constitutions NN and Nn respectively, and we back cross to normal stock, NN, any number of times, p, then the genetic composition of the last generation produced after p such back crosses will be

$$[2^p r + (2^p - 1)s]NN + sNn.$$

Since the first term becomes much larger than the second as p increases, the number of homozygous normals becomes very great compared with the heterozygous normals.

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## FURTHER OBSERVATIONS ON SEX IN MERCURIALIS ANNUA

IN an earlier paper,[1] I briefly mentioned the occurrence of so-called moncœcious forms in *Mercurialis annua*. I have since then continued my studies upon such forms and this report deals with the offspring of the so-called moncœcious plant, No. 3. It is to be noted that *Mercurialis annua* is described as appearing in

[1] Inheritance of Sex in *Mercurialis annua*, *American Journal of Botany*, Dec., 1919.

three forms, male, female and monœcious. Several hundred seeds from plant No. 3 were sown in Fargo, North Dakota, in the spring of 1919. Owing to a protracted drought only four plants survived.

In their general habit of growth these plants were like the females of my earlier observations—the flowers were clustered

FIG. 1. Branch *Mercurialis annua*. *a*, male flower bud; *b*, female flower bud; *c*, female flower; *d*, male flower; *e*, hermaphrodite flower.

in the axils of the leaves, either sessile or on more or less elongated peduncles. In another paper (Mss.) I have described in detail the various floral arrangements that appeared on these plants. Female flower buds are conical. The male buds are smaller than the female buds and they are spherical. The hermaphrodite flower buds are like the female buds though sometimes smaller. Just prior to the opening of the hermaphrodite

flower buds, the anthers may be recognized through the sepals. These four plants are not monœcious, since male, hermaphrodite and female flowers appeared simultaneously on the same plant.

Plant No. 3–1 made a vigorous growth from the beginning. Its foliage was dark green. The first flowers were female and these were produced in increasing numbers. No attempt was made to count the female flowers prior to the appearance of male and hermaphrodite flowers. As can be seen from the table the female flowers always outnumbered the male and hermaphrodite flowers. Until September 10 the male flowers were more abundant than the hermaphrodite. On September 12, there was a sudden increase in the number of hermaphrodite flowers. This rather sporadic appearance of flowers other than female flowers shows how impossible it is to determine at one time the sex of the individual. It is apparent that it is essential that such individuals be studied throughout their whole life history. Thus through the first three months of its history this plant was female, after that it was polygamous, monœcious, and gynomonœcious. It was polygamous when beside the female flowers there appeared male and hermaphrodite flowers, monœcious when only male flowers appeared in association with the female flowers, and gynomonœcious when hermaphrodite flowers appeared together with female flowers. The total number of male and hermaphrodite flowers was about equal (table). This plant may be characterized as a polygamous one.

While there were no definite points at which male or hermaphrodite flowers appeared, there were branches that continued to produce only female flowers throughout the life of the plant. Thousands of seeds were collected from the plant.

Plant No. 3–2 like plant No. 1 made a vigorous growth. Its foliage was much lighter than that of plant No. 1 but the plant was healthy. As can be seen from the table the number of male and hermaphrodite flowers that appeared at one time was relatively larger than in any of the other plants. This condition was maintained throughout the life of the plant. This plant from the time of the appearance of male and hermaphrodite flowers was decidedly polygamous, prior to that it produced female flowers like plant No. 1. During the period in which the three kinds of flowers were counted, female, male, and hermaphrodite, the male flowers were in excess. It may be conceived

then that during a part of its life history the male elements predominated. This plant was a very prolific seed producer.

Plant No. 3–3 was a very vigorous grower and it behaved like plants Nos. 1 and 2 until the time of the appearance of male and hermaphrodite flowers. The total number of male flowers when compared with the total number of hermaphrodite flowers showed that the tendency of the plant was towards monœcism. While during most of its later history male and hermaphrodite flowers appeared together, towards the end of the growing season (October 3–12) no hermaphrodite flowers were found and the plant was decidedly monœcious. This plant started out as a female, became polygamous and towards the end became monœcious. Many seed were set.

Plant No. 3–4 started out as a vigorous plant producing in the beginning female flowers in abundance. About the same time that the other plants were producing increasingly large numbers of male and hermaphrodite flowers this plant produced very few, 10 males and 4 hermaphrodites. After that the plant began noticeably to lose in vigor, the leaves began to curl up. The plant after that produced female flowers in abundance. These however dried up very quickly and dropped off. The plant continued its sickly growth until it was killed by frost.

Pistillody and staminody occurred very abundantly in the flowers of the first three plants. This condition I have described in detail in another paper (Mss.). Many of the hermaphrodite flowers had only a single stamen. The plants also produced a large number of three-carpelled female and hermaphrodite flowers whereas a two-carpelled flower is the rule.

While the number of plants is too small to warrant the drawing of any definite conclusions the following suggestive facts are brought out.

1. Sex is not a fixed condition in these forms of *Mercurialis annua.*

2. A plant may change its sex during the progress of its life cycle.

3. Continued study with larger numbers of such plants will very likely show marked variations and sex intergradations and that a strict category of sex for these forms is untenable, so that the terms monœcious, gynomonœcious, gynodiœcious, etc., can be only arbitrarily employed.

| Plant | May 25 to Aug. 25 | Aug. 27 | | | Aug. 30 | | | Sept. 1 | | | Sept. 4 | | | Sept. 8 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Only ♀ Flowers Produced | ♀ Fls. | ♂ Fls. | ☿ Fls. | ♀ Fls. | ♂ Fls. | ☿ Fls. | ♀ Fls. | ♂ Fls. | ☿ Fls. | ♀ Fls. | ♂ Fls. | ☿ Fls. | ♀ Fls. | ♂ Fls. | ☿ Fls. |
| 3–1 | ∞ | ∞ | 11 | 2 | ∞ | 4 | — | ∞ | 5 | 1 | ∞ | 4 | 6 | ∞ | 40 | 10 |
| 3–2 | ∞ | ∞ | 25 | 6 | ∞ | 70 | 36 | ∞ | 294 | 298 | ∞ | 158 | 163 | ∞ | 282 | 126 |
| 3–3 | ∞ | ∞ | 5 | 1 | ∞ | 3 | 4 | ∞ | 2 | — | ∞ | 9 | 4 | ∞ | 15 | 9 |
| 3–4 | ∞ | ∞ | — | — | ∞ | 1 | — | ∞ | 6 | 4 | ∞ | — | — | ∞ | 3 | — |

| Plant | Sept. 10 | | | Sept. 12 | | | Sept. 16 | | | Sept. 18 | | | Sept. 22 | | | Sept. 25 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | ♀ Fls. | ♂ Fls. | ☿ Fls. | ♀ Fls. | ♂ Fls. | ☿ Fls. | ♀ Fls. | ♂ Fls. | ☿ Fls. | ♀ Fls. | ♂ Fls. | ☿ Fls. | ♀ Fls. | ♂ Fls. | ☿ Fls. | ♀ Fls. | ♂ Fls. | ☿ Fls. |
| 3–1 | ∞ | 18 | 8 | ∞ | — | 150 | 580 | 50 | 40 | | | | 120 | 40 | — | 200 | 20 | 100 |
| 3–2 | 750 | 700 | 450 | 750 | 850 | 550 | 590 | 650 | 350 | 301 | 550 | 512 | | | | 165 | 225 | 60 |
| 3–3 | ∞ | 22 | 4 | 220 | 220 | 60 | ? | 20 | ? | 60 | 200 | 50 | 120 | 340 | — | 180 | 110 | 30 |
| 3–4 | | | | | | | | | | | | | | | | | | |

| Plant | Sept. 27 | | | Oct. 3 | | | Oct. 12 | | | Total | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | ♀ Fls. | ♂ Fls. | ☿ Fls. | ♀ Fls. | ♂ Fls. | ☿ Fls. | ♀ Fls. | ♂ Fls. | ☿ Fls. | ♀ Fls. | ♂ Fls. | ☿ Fls. |
| 3–1 | 102 | 91 | 24 | 500 | 100 | — | 1000 | 200 | 200 | ∞+2502 | 583 | 541 |
| 3–2 | 130 | 130 | 80 | 400 | 480 | 500 | 360 | 480 | 120 | ∞+3446 | 4892 | 3251 |
| 3–3 | 340 | 360 | 20 | 200 | 50 | — | 800 | 400 | — | ∞+1920 | 1906 | 182 |
| 3–4 | | | | | | | | | | ∞ | 10 | 4 |

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## COMMENTS ON A RECENT CHECK-LIST

RESEARCH stations established in the past by scientific institutions, especially those in or near the tropics have generally been devoted particularly to study of aquatic organisms. It was, therefore, with great pleasure and with high hopes for its future that naturalists all the world over have watched with keenest interest the establishment and gradual development of the Tropical Research Station of the New York Zoological Society.

Mr. Beebe has shown great acumen in selecting his locality. His facile pen has drawn the wonders of his station's environment in a way so splendidly vivid that I, for one, envy very frankly his skill and his good fortune. These comments then are offered here, on one of his recent papers, with a cordial appreciation of the debt which all naturalists owe to him for what should in the future become the most useful workshop of its kind: indeed to be thought of always in future as bearing a relation to the tropic rain-forest in the same way that one subconciously recalls the Naples Station when thinking of or discussing the fauna of the Mediterranean Sea.

Beebe has charmed many readers with essays which show that he is gifted with a delightful diction and a romantic style most convincing and hence to be most carefully used. To criticize these essays unkindly is far too much like picking apart an orchid. Nevertheless they sometimes have the defect of capitalizing supposed "new discoveries" at a rather high advertising value when the history of our earlier knowledge has not been determined from the literature.

Thomas Penard, in an article of marked gentleness and courtesy,[1] has reviewed Beebe's "Tropical Wild Life," in such a way that further elaboration is happily unnecessary. Now, however, articles have appeared in *Zoologica*,[2] which require more careful examination. They purport to be usable lists, admitted to be necessary, for any study of the higher vertebrates of British Guiana with special reference to the fauna of the Bartica district —the species which Beebe has actually found there being starred with an asterisk.

Beebe introduces them as follows:

> Finding no résumé available of the Amphibia, Reptilia and Mammalia of this colony, I have gone through the literature at hand and made my own lists. These I offer as a preliminary enumeration of the species thus far recorded in literature, or in my own collections, from this British Colony. They form a tangible basis for future increments—the many new species and the radical extension of present known distributions which intensive study of these phyla in British Guiana is certain to achieve. *Check-lists of mere names such as these are wholly foreign to the future zoological work of the Tropical Station* (italics mine), but they are *absolutely necessary* as a basis for identification and investigation, and it is in this spirit that this preliminary work has been undertaken.
>
> I have made no attempt at a thorough search of literature for priority or for confirmation of names or other similar phases of taxonomy, deeming this the special province of the literary systematist. I have merely sought to utilize the most recently accepted names of herpetologists and mammalogists.

Now, generally speaking, the "literary systematist" does not confine himself to this somewhat dry but entirely necessary vocation, wholly from choice and he is saddened when his more foot-free colleagues cast supercilious glances his way. It therefore

[1] *Auk*, 36, 1919, pp. 217–225.

[2] Vol. 2, Nos. 7 and 8, 1919.

behooves the now deservedly but still very highly vaunted "FIELD NATURALIST" to write with care when he deliberately invades the province of his more lowly associate. Systematists know that the preparation of a good, useful check-list of a region like British Guiana is no task to be entered upon lightly nor unadvisedly and because the work is not spectacular, arouses little popular acclaim and is slow and tiresome, we sometimes wonder whether these facts have not a high value in explaining the rather supercilious and scornful appraisal given to a mere check-list by the modern field naturalist. Admittedly, however, this work if worth doing at all, is worth doing well but this list of Beebe's is so phenomenally bad that we are loath to believe that Mr. Beebe has tried to make it even moderately good. For example, in so far as reptiles and amphibians—or mammals—are concerned there is no evidence that specimens of many of the obscure species discussed have ever been preserved for examination by a herpetologist.

We read of *Bufo molitor*. This name was given by Tschudi[3] to a toad from high Peru. Naturalists in recent years have so far as I know felt reasonably sure that this was a synonym of *Bufo marinus* pure and simple. Stejneger has said recently:

> Whatever may be the status of Tschudi's *Bufo molitor* the half grown toad [taken by the Yale Peruvian Exp.] collected at Santa Ana . . . unquestionably belongs to *Bufo marinus*.

So also all the Peruvian examples collected by Mr. G. K. Noble and now in the M. C. Z., Cambridge. Here then this name appears resurrected in literature and recorded from Bartica, of all places, and no proof whatsoever offered to support so wholly improbable a statement.

*Bufo sternosignatus* Keferst. The types came from western Venezuela and Colombia. Günther's figure of this species shows how easily it also might be taken for the young *Bufo marinus*. Since apparently the species is not known from eastern South America can this be called a valid record until Beebe's specimen, if it was preserved, falls into a herpetologist's hands?

*Hyla indris* Cope. Another species, known apparently only from Cope's original description which strongly suggests that it was probably nothing but an individual variant of *Hyla crepitans*.

[3] Fauna Peru, Herp., 1845, p. 73, Pl. 12.

*Hyla punctata* of Beebe's list is probably *Hyla helenæ* Ruthven, described *from British Guiana* and evidently *entirely unknown* to Beebe.

*Hyla fasciata* here definitely recorded from British Guiana although not captured (no asterisk), hence the record is probably copied from Boulenger's Catalogue, where there is a large question mark which is here omitted.

*Hyla lineomaculata* Werner is yet to be proved distinct from *Hyla rubra.*

The *Ceratophrys cornuta* starred as having actually been taken would indeed have been a prize had it fallen into appreciative hands. For the finding of this species so far from home would be worth most painstaking verification. Has Mr. Beebe saved the specimen? It is not in the American Museum in New York, whose reptile series suffers sadly through Beebe's scorn of the collector.

Specimens must be seen before the records of *Leptodactylus longirostris* Boulenger (type locality Santarem), *Leptodactylus ocellatus* (Linné), widespread in the southern South American grasslands and *Leptodactylus gaudichaudii* can be considered.

Suddenly using capitals for specific names, perhaps in a burst of enthusiasm at the shock which he knows the "closet naturalist" will suffer, we read that he has found Otophryne "Robusta" at Bartica, so also Atelopus "Proboscideus," Atelopus varius and Atelopus pulcher. In the same category of most highly improbable records, among others, we find *Anolis ortonii* of the Peruvian montaña and *Anolis sagrei* a native of Cuba and the Bahamas. *Ameiva surinamensis* is referred to in an adjoining paper correctly as *Ameiva ameiva,* we wonder if they are considered the same species. *Prionodactylus* we had always supposed to be a characteristically Andean genus yet here the Equadorian oshaughnessyi appears as actually occurring at Bartica! *Cophias* should appear as *Bachia* but Beebe would probably consider this as "in the special province of the literary systematist" or is this simply a case of where Mr. Tee-Van, in his "untiring search" of the literature, got too tired before the pertinent reference was found? The boas' names are rather confused as we use them now—another purely literary matter, however. The nomenclature of the snakes in general is a mixture of earlier usage with the acceptance of such a radical concession to necessity as the use of *Micrurus* for *Elaps,* while in many other cases

no attempt has been made to follow the now generally accepted canons of the International Code of Zoological Nomenclature.

It is hard to review a paper of this sort without being personal, for personality becomes most inexplicably pushed into what at first sight is pure dry-as-dust. It is only fair to offer constructive criticism also in such a case as this. Beebe should first learn the value and importance—and the use—of an adequate library. He should have attached to his staff trained taxonomists who are also skillful collectors. These men should, taking the fauna group by group, make careful determinations so that the observers at the station may know what they are working with. Any reliance in the future on such a list as the one published—admitted to be necessary—yet "wholly foreign" to the station's aim—will be regarded by sincere naturalists with pity at the great opportunity lost and sorrow at the misuse of resources and energy.

We may point our moral and adorn our tale with the wish that: when that "little Danish flapper" in St. Thomas taught Beebe that lizards may be noosed as he tells us, "Thus after years of effort" we wish that instead of only showing him what every reptile collector learns from the first urchin he meets, if he has not already devised the scheme by instinct, be the urchin yellow, red, white or black, that she had said "Oh, kind Sir! Do *keep the lizard* for your less happy colleagues at home will still have much to learn from that poor despised little pickled carcase."

THOMAS BARBOUR